ASPECTS OF THE ENERGETICS AND RENAL PHYSIOLOGY OF SOME AFRICAN ARID-ADAPTED RODENTS.

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DECLARATION

The work contained in this thesis is my own in concept and, for the most part, in execution. Naturally I have held discussions with several colleagues during the course of the studies reported here. This, and all technical assistance I have had, is fully acknowledged in this thesis. No part of this work has been submitted before for any degree or examination in any other university.

R. Buffenstein

R. BUFFENSTEIN

ABSTRACT

The following aspects of physiological adaptation and resource usage were examined in several species of arid-adapted African rodents:

The effect of temperature on thermoregulation, metabolism, evaporative water loss and thermal conductance was studied in the North East African pigmy gerbil, _Gerbillus pusillus._ This gerbil did not strictly maintain homeothermy and like most arid-adapted rodents had a reduced basal metabolic rate. When _G. pusillus_ was maintained on an _ad lib._ food and water diet, its daily energy expenditure was similar to that predicted by mass. This increased to 116% of the expected allometric value when deprived of water. On a diet of air-dried millet seeds, increased kidney concentrating ability, reduced pulmocutaneous evaporation and a reduction in faecal water loss, were sufficient to impart virtual independence of exogenous water and the maintenance of a positive water balance.

If food was restricted, _G. pusillus_ utilized torpor to precisely balance energy expenditure with that available and so maintained a constant body mass. During torpor, assimilation efficiency was significantly reduced. The cost of maintaining coenothermia

for the full duration of food processing would be prohibitive and it was estimated that it would have utilised approximately 50% of the daily energy available. The cost of employing torpor (0.5kJ.day^{-1}) on the other hand was insignificant in comparison with the savings accrued by the use of torpor (32.25kJ. day^{-1}). Parsimony of water loss with food restriction enabled the maintenance of a positive water balance during this period.

The importance of microhabitat in thermoregulation was investigated in *Gerbillurus paeba*, inhabiting the thermally stable confines of a plugged burrow, and in *Aethomys namaquensis*, a crevice dwelling rock rat. The rock rat, living in an environment characterized by large diel ranges, precisely controlled body temperature. It did this by compensating for its reduced basal metabolic rate, with a low rate of thermal conductance. *Gerbillurus paeba* tolerated a labile body temperature and used a high rate of thermal conductance to remove metabolic heat, for the high humidities it encountered in its milieu would impede the use of evaporative cooling.

Daily energy expenditure of both Namib rodents, was monitored when they were maintained on a low fibre food source (golden millet) and then when this was replaced with a high fibre food source (high-bulk bran).

Aethomys namaquensis showed a DEE similar to that predicted by mass and this remained constant, irrespective of the food source or the presence or absence of water. The DEE of G. paeba was more variable. When water was freely available DEE was higher than that predicted by mass and was similar to that predicted for an insectivore of similar body mass. This might reflect its propensity towards an insectivorous diet. When water-stressed on a high fibre diet, DEE of G. paeba declined by half, suggesting that G. paeba employed torpor when conditions were stressful and when the quality of resources was reduced.

On a low fibre diet, both species were able to maintain a positive water balance when deprived of water, showing similar reductions in water loss to that of G. pusillus. Low assimilation efficiency and the concomitant increase in faecal water loss precluded the maintenance of a positive water balance when they were fed a high fibre food source. Despite increased urine concentrations and reduced evaporative water loss both species succumbed to chronic water-deprivation.

Daily water turnovers and urine concentrating ability was monitored in 17 species of African rodents from arid areas. In general, rodents belonging to the Cricetidae exhibited lower water turnovers and voided

smaller volumes of urine at significantly greater concentrations than the murids. All these cricetid rodents were found to produce a crystalline precipitate of allantoin in their urine when water stressed. The quantities of crystalline allantoin excreted were far greater than that expected from purine catabolism and accounted for 30% of the total nitrogenous wastes of the cricetids when deprived of water. It was thought that the substantial quantities of allantoin excreted were responsible for the lower water turnover rates in the cricetids. It is suggested, therefore, when water is limiting, there is a shift in the nitrogen pathway from urea to allantoin, so conferring an eco-physiological advantage to these long term residents of the arid regions of Africa.

ACKNOWLEDGEMENTS

Many people were generous with their time and help and I have acknowledged them gratefully in the appropriate parts of this thesis. I would like to thank here, those who contributed in a more generalised way.

I extend my heartfelt thanks to my supervisor, Professor JUM Jarvis for her time, assistance and encouragement she has given me in the various phases of the work. Professor GN Louw is sincerely thanked for generously giving of his time, ideas and assessments. Many valuable discussions were had with Professor GA Bartholomew and Professor PC Withers during their visits to UCT.

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PREFACE

Deserts have been defined as "areas where the environment places insurmountable obstacles in the way of its inhabitants" (Schmidt-Nielsen, 1979). It is difficult to define precisely these 'arid-zones', for these areas are a direct result of a combination of several factors, namely temperature, rainfall and evaporation. Louw and Seely (1982) consider the most useful definition to be that suggested by Noy-Meir (1973). He has defined an arid zone as a water controlled system with infrequent discrete and largely unpredictable water inputs. Large animals inhabiting these hot hostile environments are generally nomadic, emigrating when conditions become too stressful. Rodents, by virtue of their small size, cannot migrate under these circumstances and must therefore be able to withstand prolonged periods of drought. They are forced to cope with scattered unpredictable food resources, lack of water, extremely high day temperatures and the concomitant problems of heat dissipation, and lack of cover for predator avoidance. Natural selection, being an optimising process, results in the phenotypic specifications of the animals interacting with the environment in such a way as to maximise the spread of descendents (Gould and Lewontin, 1979).

Rodents in general have shown a remarkable ability to adapt to and exploit every type of terrestial niche. The adaptability of these animals is both of medical and of agricultural importance (Taylor, 1970; Bray, 1974; Brooks, 1974; Myllymaki, 1979; Johnson et al., 1981) and consequently their eco-physiology has been the focus of much attention primarily in Europe and in North America (Robertshaw, 1974; Bradley et al., 1975; Gates and Schmerl, 1975; Golley et al., 1975; MacMillen and Christopher, 1975; Bligh et al., 1976; Hill, 1976; Johnson, 1976; Stoddart, 1979). Ecological and physiological research of African small mammals has generally been neglected. It is indeed only within the last five years that rodent eco-physiology has evoked much interest (Christian, 1979a and b; Kassir et al., 1979; Amirat et al., 1980; Christian, 1980; Perrin, 1980; Withers et al., 1980; Christian, 1981; Haim, 1981; Knight and Skinner, 1981). Prior to this period, most eco-physiological research on African rodents was restricted to renal studies conducted in the arid zones of Egypt (Burns, 1956; Khalil and Tawfic, 1963; Haggag and El-Husseini, 1965 El-Husseini and Haggag, 1966; Haggag et al., 1968; Khorshid et al., 1969; El-Husseini and Haggag, 1974; Haggag and El-Husseini, 1974; Mostafa et al., 1975; Moussa et al., 1977).

During an investigation on the adaptive renal efficiency of three species of rodent from the Namib desert, it was observed that the two cricetid species, *Gerbillurus paeba* and *Gerbillurus tytonis* responded differently to water-stress than the murid, *Rhabdomys pumilio* (Buffenstein, 1977). Consequently other aspects of adaptive physiology were examined in several species of both murid and cricetid rodent from the Namib desert and from the arid zones of north-eastern Kenya. This thesis is concerned with these physiological adaptations and is presented as a series of papers. As the papers had to comply with the requirements of the different scientific journals to which they were submitted, editorial inconsistencies are evident. The most obvious of these concern the format of the reference lists at the end of each chapter.

The chapters can be essentially divided into six parts. Part one (chapter 1) gives a general introduction to the animals and includes information on their taxonomy, distribution and social structure and alludes also to the available literature on African rodents. This section will not be submitted for publication. Part two (chapters 2 to 4) is concerned with the eco-physiological adaptations of the smallest African gerbil, *Gerbillus pusillus*, to available resources and to temperature fluctuation. This section examines firstly, their basal metabolic rates and thermoregulatory ability. In addition, the conditions resulting in the employment of torpor and problems associated with torpor are investigated. Part three (chapter 5) deals with thermoregulatory problems which might be exacerbated by microhabitat. This is done by comparing basal metabolic rate, evaporative water loss, thermal conductance and lability of body temperature in two Namib desert rodents: a crevice dweller, Aethomys namaquensis, and a semi-fossorial burrow dweller, Gerbillurus paeba. Part four (chapter 6) examines the importance of the quality of food and resource selection when water is limited. This is done by monitoring both energy and water balance when the rodents are maintained on a low and high fibre diet. The energy and water requirements of a crevice dwelling murid, A. namaquensis are compared also to that of a semi-fossorial cricetid, G. paeba. The taxonomic differences in nitrogen excretion and renal efficiency of 22 species from both arid and mesic areas are discussed in part five (chapter 7), which is followed by the Summary and Conclusions.

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PART 1

CHAPTER 1

The study animals; their distribution and habitat.

The study animals

Whilst fourteen species of rodents from the arid zones of both North Africa and South West Africa were collected and used in this thesis, only background information for the three species examined in detail is given here.

Taxonomy

The arrangement of the African subfamilies within the Cricetidae and Muridae is at best confusing (Swanepoel *et al*., 1980) and is in dire need of revision (Missone, 1974; Davis, 1975; Schlitter, 1978; Chaline and Mein, 1979). The classification used throughout this thesis follows that of Davis (1975), in which the African cricetids are assigned to a separate family from the murids.

Both *Gerbillurus paeba* and *Gerbillus pusillus* are members of the Gerbillinae. Much confusion still exists in the taxonomy of this group. Whilst treated as a subfamily of the Cricetidae, they themselves may warrant family rank. This has been suggested by Petter (1966) and more recently by Chaline and Mein (1979). In addition, Petter (1971), Schlitter (1976) and Osborn and Helmy (1980) stress that modern methods of taxonomy are required to separate the closely related species.

The taxonomy of the East African Gerbillinae subgenus Hendecapleura was revised by Roche (1975). He suggested that the following are merely synonyms for *Gerbillus pusillus* (Peters 1878):- *Gerbillus ruberrimus* (Rhoads, 1896), *Gerbillus diminutus* (Dollman, 1911a) and *Gerbillus percivali* (Dollman, 1914a). However, there is still much controversy concerning the inclusion of *G. ruberrimus* into this species (Yalden *et al.*, 1976; Rupp, 1980). Roche (1975) admits himself that a proportion of the specimens of *G. ruberrimus* cannot be allocated with much certainty. Yalden *et al.* (1976) and Rupp (1980) therefore have excluded *G. ruberrimus* from this species. Only *G. pusillus* from Somalia has been karyotyped (Capanna and Merani, 1981). Once other morphologically similar gerbils are karyotyped, species allocation will become easier.

Gerbillus pusillus are recognised by their small size (8-18g), naked soles, normal tympanic bullae and fawn coloured dorsal fur.

Gerbillurus was considered a subgenus of *Gerbillus* by Shortridge (1934; 1942) and Ellerman *et al.* (1953).

However Roberts (1951), Davis (1975), Schlitter (1976) and Swanepoel *et al*. (1980) have elevated it to generic rank. *Gerbillurus* differs from *Gerbillus* in that bullae are more inflated (Davis, 1975). Schlitter (1976) has shown that it is phylogenetically closer to *Tatera* than to *Gerbillus* after comparisons of the enamel patterns of the molars and molar alveoli of the different genera. This genus is in urgent need of revision (Coetzee, 1972; Schlitter, 1973). *Gerbillurus paeba* was thought to be a synonym for *Gerbillus gerbillus* by Ellerman *et al*. (1953). However, Herold and Niethammer (1963) disagreed with them as have several other more recent authors. At present the following species are thought to be synonyms for the hairy footed pigmy gerbil:- *Gerbillus broomi*, *Gerbillus calidus*, *Gerbillus kalaharius*, *Gerbillus leucanthus*, *Gerbillus mulleri*, *Gerbillus oralis*, *Gerbillus swakopensis* and *Gerbillus swalius* (De Graaff, 1981). These gerbils are recognised by; their slender form, weight (21-35g), hairy distal part of their hind feet, slightly tufted longish tails, grooved upper incisors, well developed ears and the fact that the posterior portion of their bullae are not conspicuously developed (Davis, 1975; De Graaff, 1981).

Smithers (1971) and Schlitter (1978) consider that the genus *Aethomys* is also in need of taxonomic revision. This species was originally placed under *Praomys* by

Thomas (1915). Ellerman (1941) regarded *A. namaquensis* as belonging to the genus *Thallomys* and considered all African rats to be closely allied. At the moment, the Namaqua rock rat, *A. namaquensis* is included in the sub-genus *Micealamys* (Davis, 1975). There are sixteen synonyms for this species (Davis, 1975). *Aethomys* may be recognised by their size, (33-75g), mottled ochre and grey dorsal fur and their ventral white fur. The fur is fairly long and soft. In addition the tail is proportionately very long and is covered with fine and closely spaced conspicuous scales and short fine bristle like hair (Smithers, 1975).

Evolution

The African desert fauna contains the second most complex assemblage of rodents in the world, the first being that of the deserts of North America (Mares, 1980). This high diversity may be due, in part, to the the formation of desert refugia during the Pleistocene (Schlitter, 1976). World arid zones attained their pronounced aridity with the orogenic activity of the Miocene and Pliocene periods (Tchernov, 1975). Gerbilline fossils date back in North Africa to the the late Pliocene and early Pleistocene (Lavocat, 1978). Since that period, the continental land mass of Africa has enjoyed greater stability of climate and geology than most parts of the world, allowing an enormous time for the evolution of a suite of adaptive morphological physiological and ecological characteristics and for the establishment of complex and stable biological communities. This long term stability has undoubtedly greatly influenced the composition of the present fauna (Moreau, 1952; 1963).

No work appears to have been done concerning rodent fossils in the Namib (M. Avery, pers com.). It is, however, generally conceded that the cricetids have had a longer evolutionary history in this area than have the murids. Lavocat (1978) has traced the African cricetid origin to the Asian cricetodonts of the Miocene and believes that the Murinae also originated in Asia from cricetodont stock, but arrived in Africa later. Coetzee (1969) came to similar conclusions. Missone (1969) suggested that Cricetidae in general are in a regressive position in comparison with the Muridae and that it is only their extreme specialization and adaptation to the more unfavourable niches that have ensured their survival.

Distribution

Apart from the records of a number of early collections in Kenya and Ethiopia (Dollman, 1911a and 1911b; 1914a;

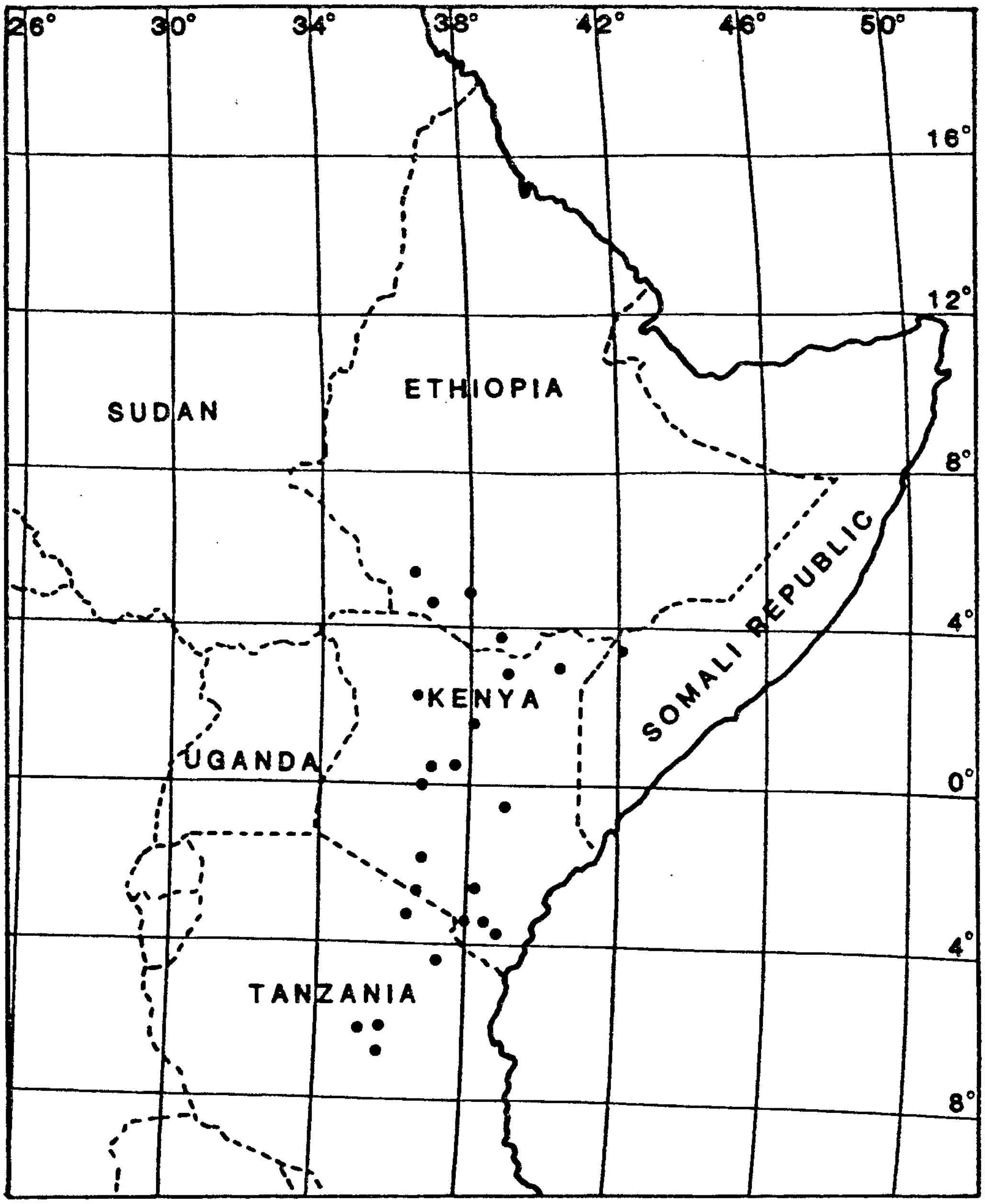


Figure 1 : Recorded distribution of *Gerbillus pusillus* (W. Peters, 1878)

Hollister, 1918; 1919; Saint Leger, 1935; 1937; Thomas, 1900) sparse information is available on the distribution and ecology of the small mammals in the more arid regions of north east Africa (Roche and Petter, 1968; Coe, 1972; Hubert, 1978). It is not possible to demarcate the distribution of small mammal species in this area with any degree of confidence; nevertheless, Fig. 1 indicates the known distribution of *G. pusillus*. The Gerbillinae occur mostly in the arid zones and to a lesser extent in the grassland savannas of tropical Africa (Delany, 1972; Delany and Happold, 1979). *Gerbillus pusillus* is no exception and has a more or less endemic distribution in arid parts of tropical East Africa: It has been recorded in southern Ethiopia (Hubert, 1978), south western Somalia (Capanna and Merani, 1981), in the open scrub savanna in the Voi district of Kenya (Dollman, 1911a; 1914b; Peters, 1878) and into northern Tanzania (Hubbard, 1972). Cockrum and Setzer (1976) have no records of *G. pusillus* in the countries where they conducted their surveys, namely:- Algeria, Egypt, Libya and Tunisia. *Gerbillus pusillus* in this study, were collected near Archers Post in N.Kenya (approximately 0°38'N, 37°40'E).

Distribution records for Southern African small mammals are more complete than their North African counterparts. Both *A. namaquensis* and *G. paeba* have

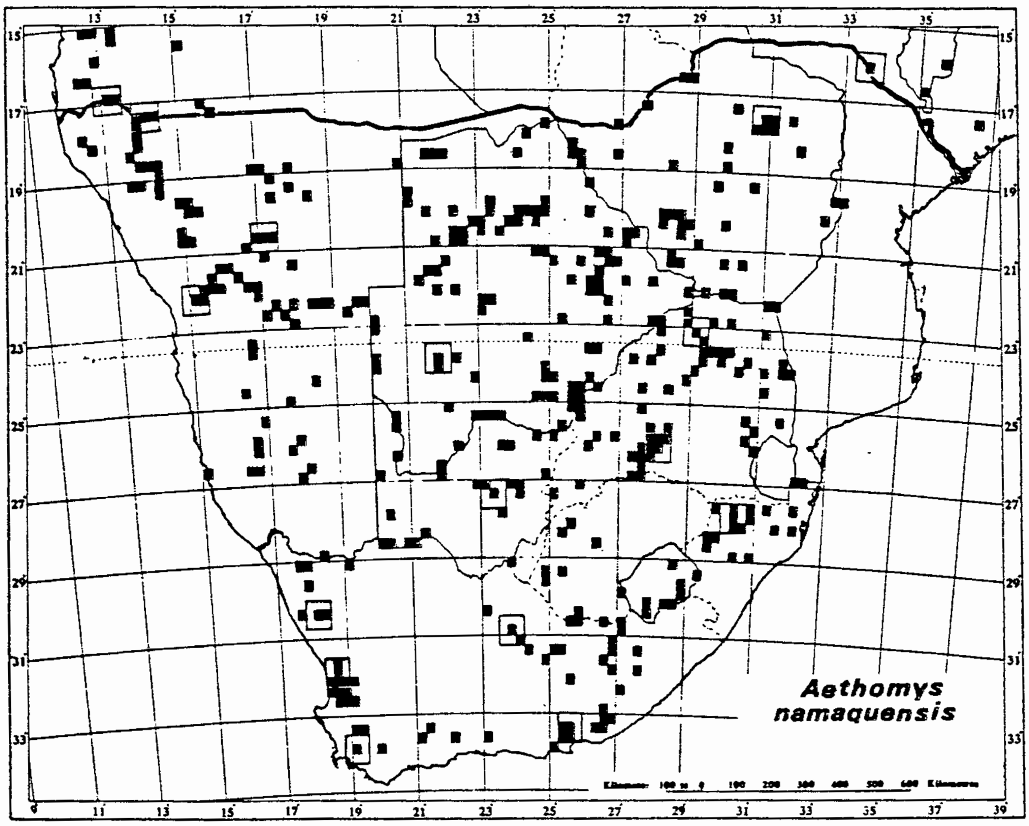


Figure 2 : Recorded distribution of *Aethomys namaquensis*
(A. Smith 1834) (from Davis, 1974)

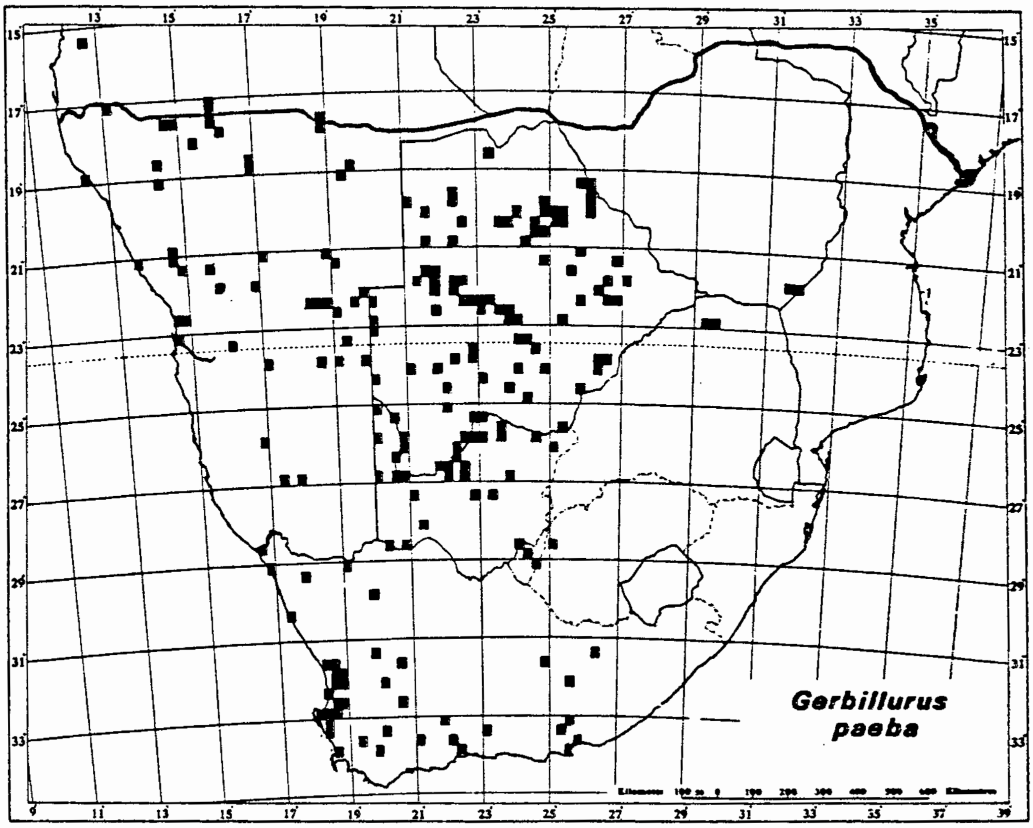


Figure 3 : Recorded distribution of *Gerbillurus paeba* (A. Smith 1836) (from Davis, 1974)

comparatively wide distributions (Figs. 2 and 3, taken from Davis, 1974). *Gerbillurus paeba* is found throughout the drier parts of southern Africa, ranging along the south coast from the Alexandra district in the Eastern Cape to the Cape Flats. From there, their distribution moves inland and northwards into the Namib desert of both SWA/Namibia and Angola, the Kalahari and into the relict patches of Kalahari sand to the north of Soutpansberg in the Tranvaal (Coetzee, 1969; Davis, 1974). *Gerbillurus paeba* is not associated with densely vegetated river beds and rocky areas and favours sparsely vegetated sandy areas. *Aethomys namaquensis* on the other hand is only associated with rocky areas (Davis, 1962; 1975; Stuart, 1975; De Graaff, 1981). It too has a wide distribution (Fig. 3) and is commonly found throughout southern Africa, south of the Zambezi except in the central regions of the Karoo and the northern coastal areas (Smithers and Lobao-Tello, 1976). It does however extend across the middle of the Zambesi into south eastern Zambia and southern Malawi. *Aethomys namaquensis* is abundant on the inselbergs in the southwest, west and northwards into west-central Angola to Pungo Andongo (Davis, 1975). Southern African rodents were collected in the Namib Park (Fig. 4). In this study *A. namaquensis* was collected at Tumasberg (23°29'S, 15°32'E) and at Groot Tinkas (22°50'S, 15°26'E) whilst *G. paeba* was collected near Gobabeb (23°34'S, 15°03'E), near Swartbank

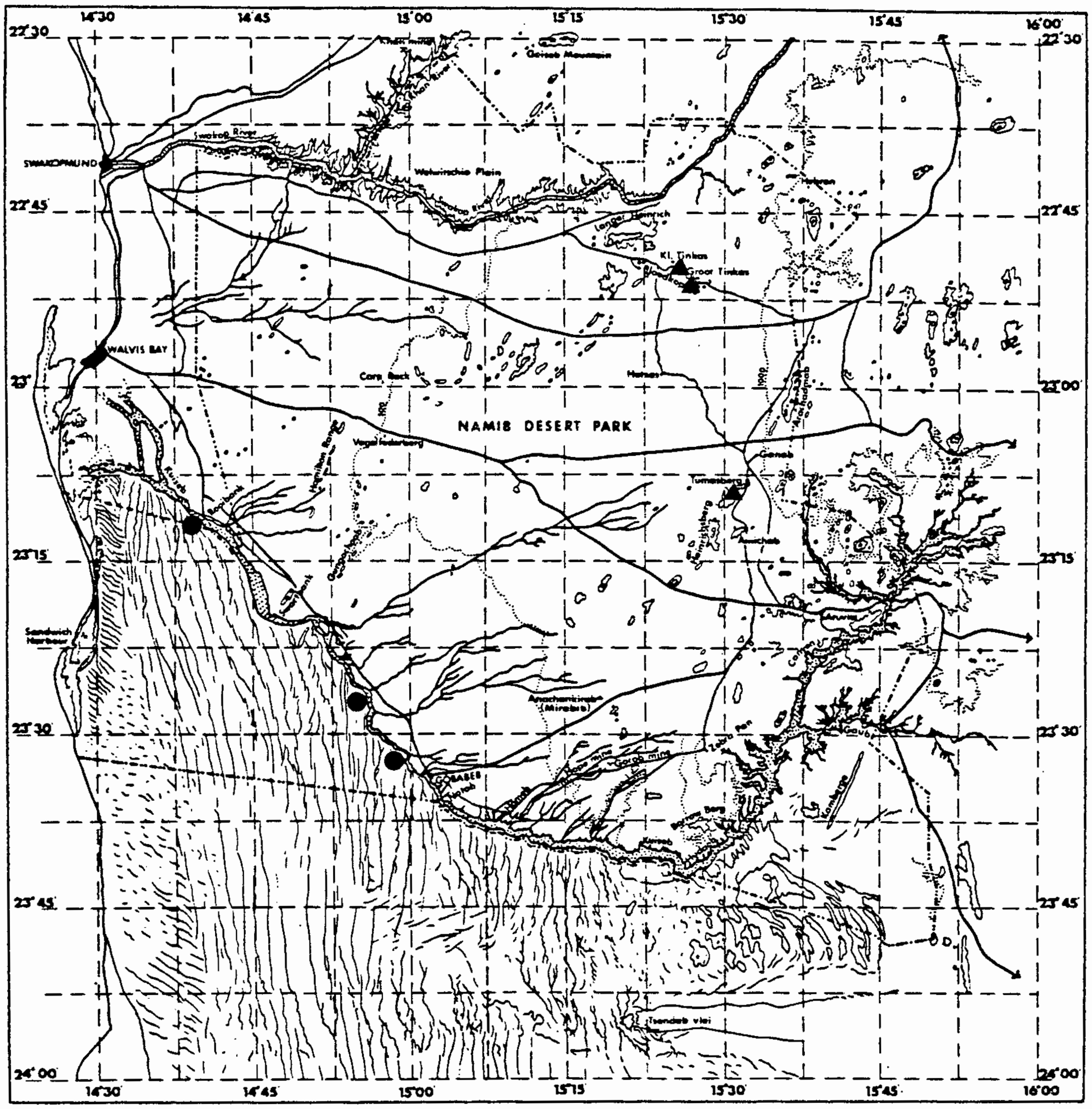


Figure 4 : Areas in the Namib desert where *Aethomys namaquensis* (▲) and *Gerbillurus paeba* (●) were collected

(23°20'S, 14°50'E), and near Rooibank (23°10'S, 14°35'E).

Geology

The three areas where the rodents were collected are geologically different (Fig. 5). The geology of the north east African site resulted from Tertiary and more recent laval flows of olivine basalt (Cooke, 1978). This gives rise to a plateau of poorly structured and excessively drained volcanic soils. These soils (Fig. 6) are generally shallow with a low available water capacity. In some places, though, other superficial materials may overlie these laval flows and result in deep, almost structureless, soils of a brown calcimorphic type (Young, 1976). However, G. pusillus appear to occupy the shallow, lighter sandy and dust like soils (Hubert, 1978). Coe (1972) found this species to be restricted to the eroded Plio-Pleistocene alluvial sediments near lake Turkana.

As both A. namaquenis and G. paeba have a fairly wide geographical distribution, only the Namib desert, where they were collected is described. The Namib desert comprises a relatively narrow tract of land, mostly less than 200km wide and approximately 2000km long (Louw, 1972). This area lies west of the escarpment

Figure 5 : Geological Map of Africa (from Clark, 1967)

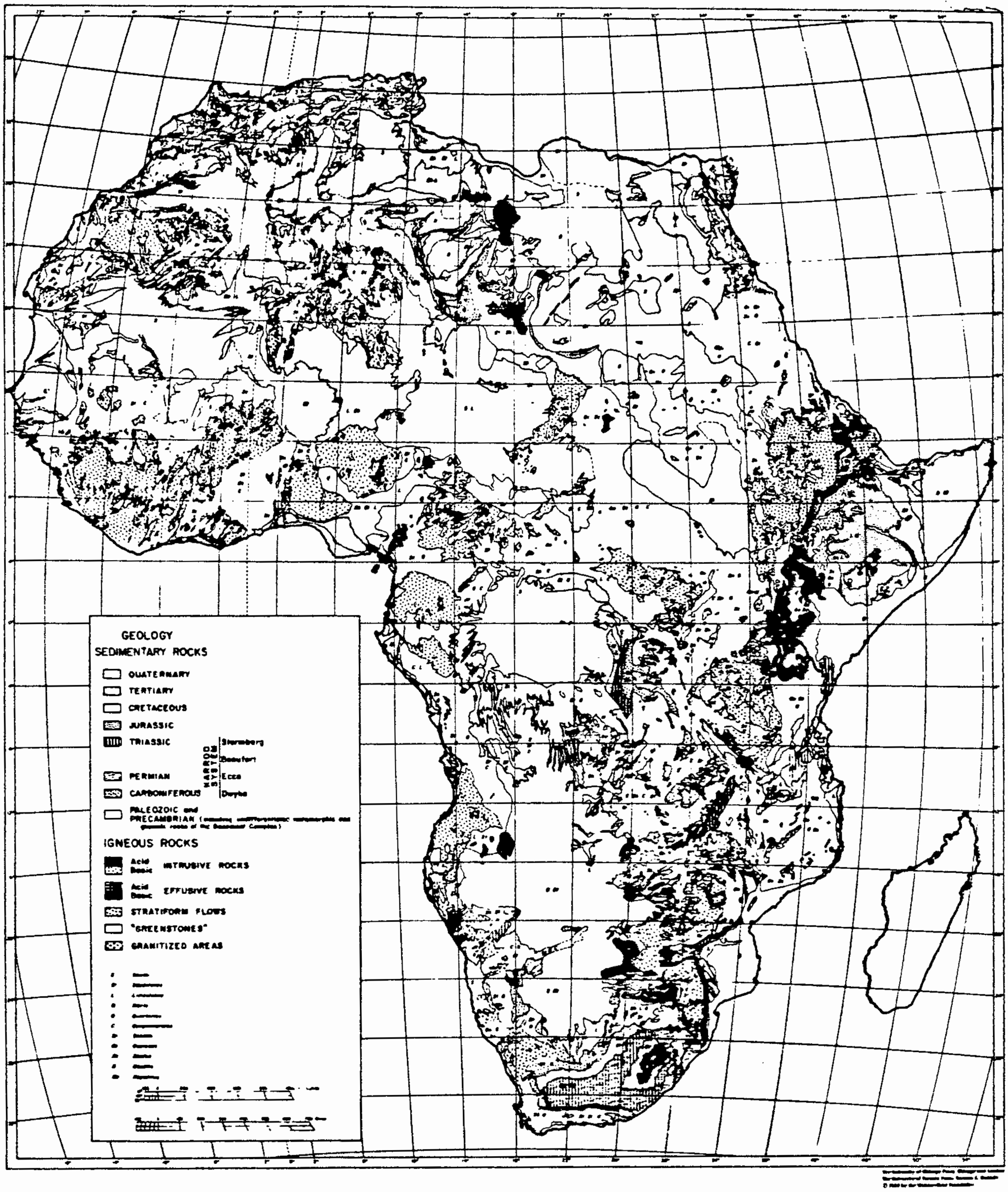
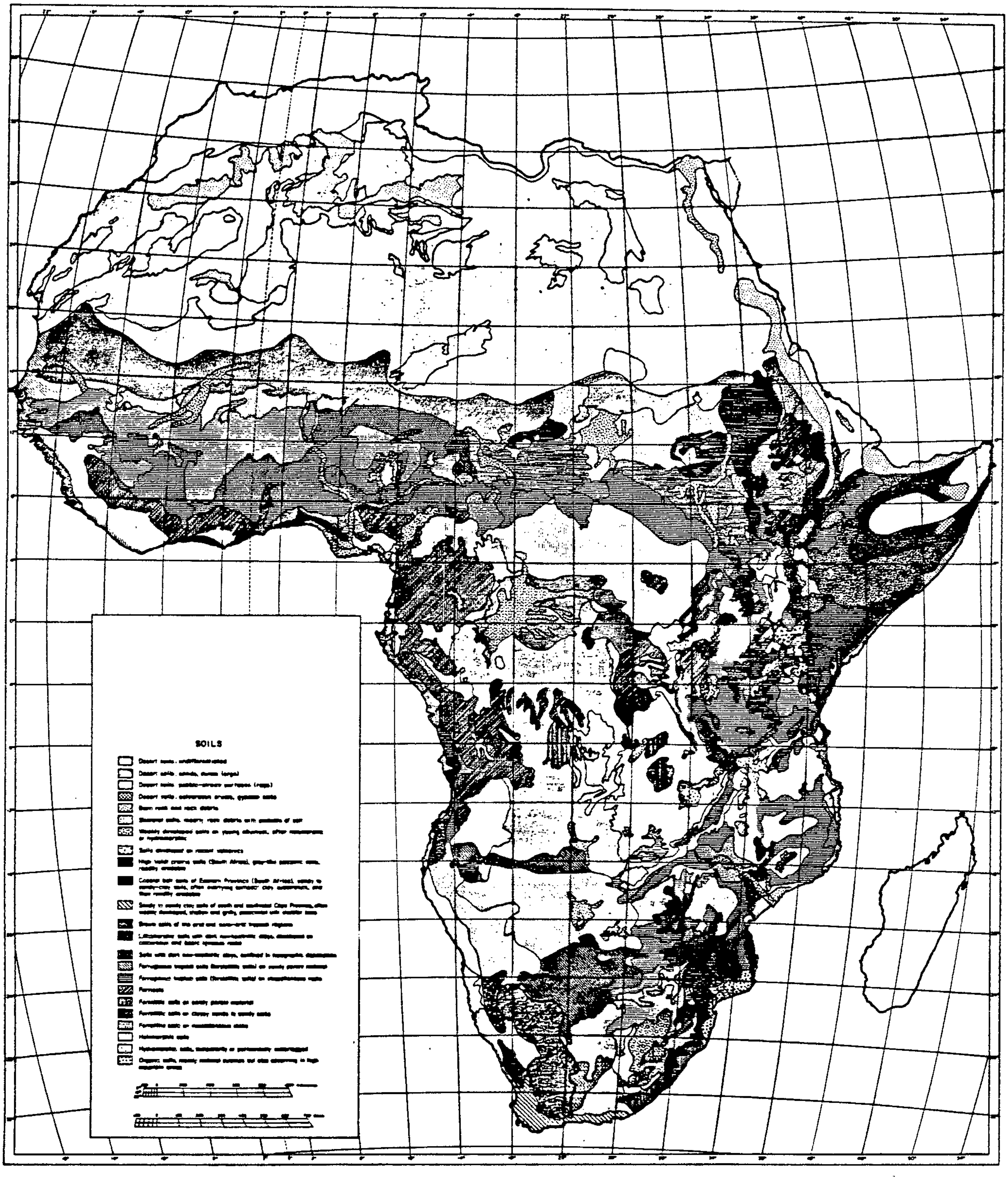

GEOLOGY
SEDIMENTARY ROCKS
QUATERNARY
TERTIARY
CRETACEOUS
JURASSIC
TRIASSIC
PERMIAN
CARBONIFEROUS
KARROO SYSTEM
Stormberg
Beaufort
Ecca
Dwyka
PALEOZOIC and PRECAMBRIAN
IGNEOUS ROCKS
Acid
Basic
INTRUSIVE ROCKS
Acid
Basic
EFFUSIVE ROCKS
STRATIFORM FLOWS
"GREENSTONES"
GRANITIZED AREAS

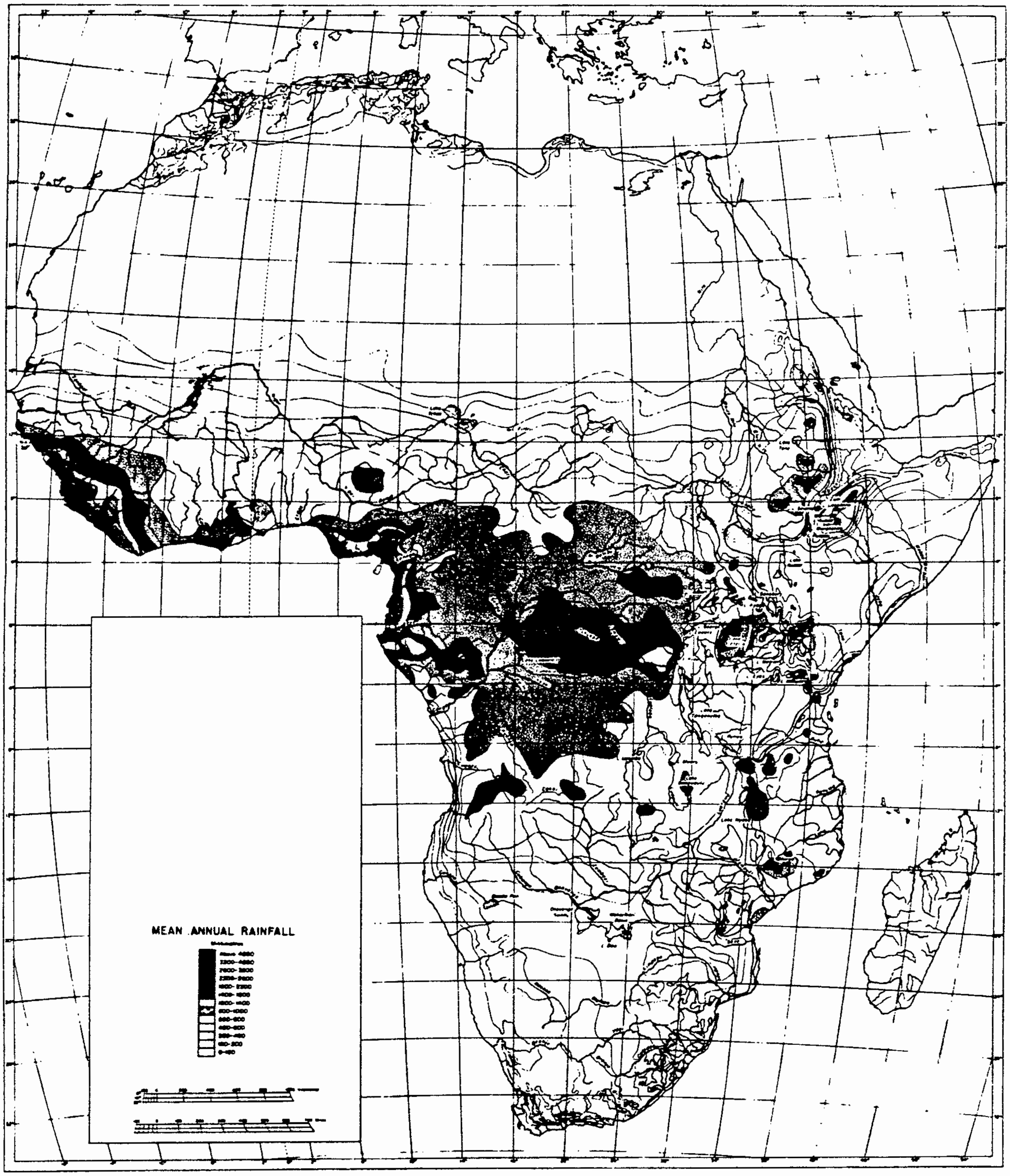
Figure 6 : Map of Africa showing different soil types (from Clark, 1967)


SOILS

between the Oliphants river (Cape Province) and the Carunjamba river (Moçamede district, Angola). The region is not homogenous, but includes a wide variety of geomorphologically different environments, notably sand seas, sand dunes, gravel plains, inselbergs and coastal salt flats, pans, ephemeral rivers and streams.

Aethomys namaquenis usually lives in cracks and crevices on the rocky inselbergs or in piles of stones on low lying ridges (De Graaff, 1981). These inselbergs consist of granite, granite-gneiss, mica schists, dolerite, feldspar formations and often lime deposits (Logan, 1960) and are thought to be of Jurassic age (Ollier, 1977). The age of the sand dunes is less certain. However, their formation is thought to have been started in the Oligocene by south to south easterly paleo winds mobilising and depositing aeolian sands (Ward *et al*., 1983). These sands consist primarily of quartz and felspar, with their charateristic reddish colour due to the ironhydroxide coating around the mineral grains (Scholz, 1972). The sands overlie a bed-rock platform thought to be sediments of the Cretacious age (Fig. 5).

Figure 7 : Climatic Map of Africa (from Clark, 1967)



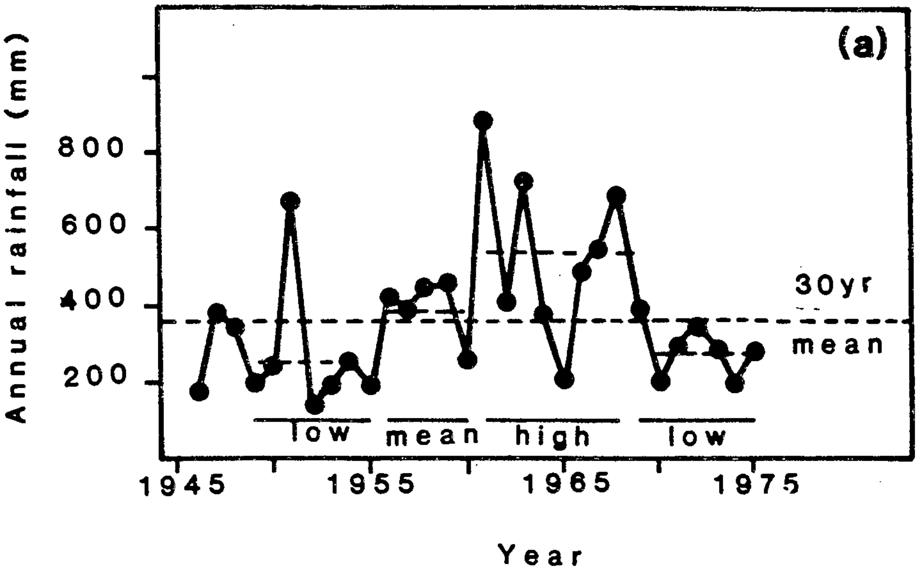
MEAN ANNUAL RAINFALL
Millimetres
Above 4000
3200-4000
2600-3200
2200-2600
1800-2200
1400-1800
1000-1400
800-1000
600-800
400-600
200-400
100-200
0-100

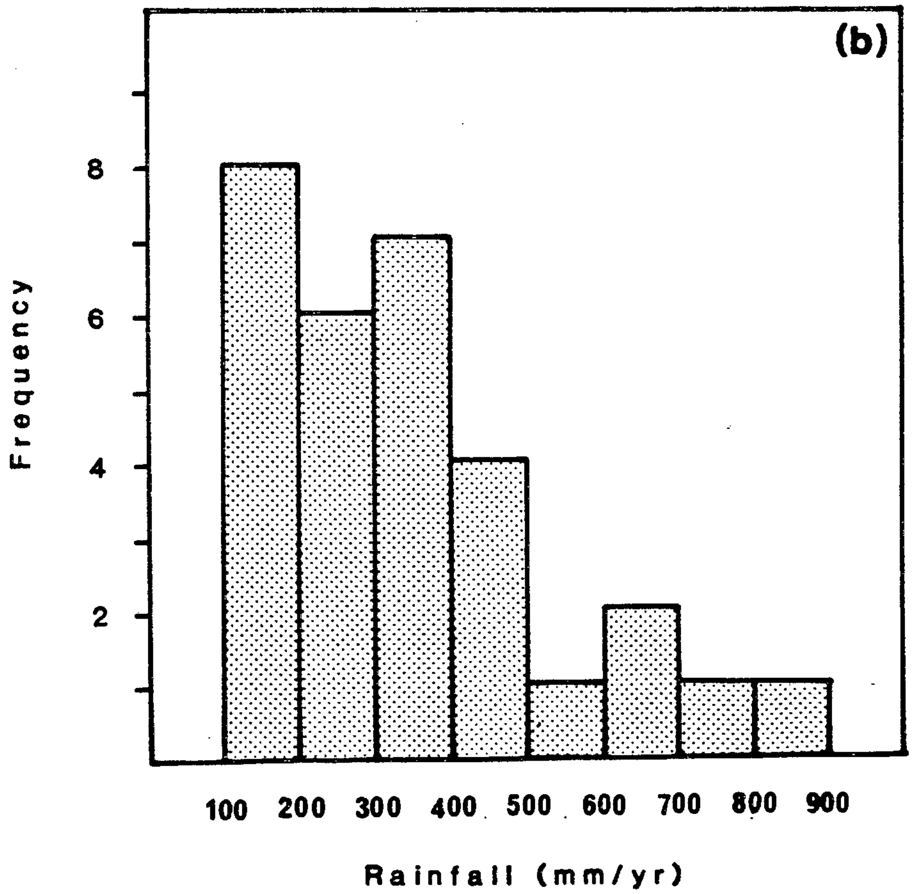
Climate

Mean monthly temperatures of the tropical zones (15°N-15°S) do not show much seasonal fluctuation (Owen, 1976). Cloudsley-Thompson (1969) reported that no cold season exists in the arid zones of tropical Africa and that the minimum monthly temperature seldom falls below 18°C. The mean monthly temperature over a wide area between northern Kenya and southern Ethiopia, varies by as little as 0.5°C (Coe, 1972). Coe (1972) found the mean monthly temperature at Lokori (1° 57'N; 35°37'E) to be 29.8°C. Daily temperature fluctuations were, however considerable, with a diel range of 19°C. Even in the cooler season a diel range of 16°C was observed (Jarvis unpubl. data).

The arid regions of North East Africa are shown in Fig. 7 (Clark, 1967). The mean annual rainfall over 30 years, from 1946-1976, for Archers Post was 354mm (Barkham and Rainy, 1976), slightly exceeding the rainfall levels characteristic of deserts (<300mm). However, the rainfall is extremely unreliable. Its' variation from year to year may be as much as 250% of the mean. The annual rainfall has only fallen within 50mm of the mean in seven of the 30 years monitored (Fig. 8). Rainfall is essentially bimodal, with peaks usually in April and November.

Figure 8 : Annual rainfall totals for Archers Post 1946 - 1975; (a) year to year variation with the dotted lines to show the means for different periods; (b) frequency histogram totals (from Barkham and Rainy, 1976)


(a)
Annual rainfall (mm)
800
600
400
200
30yr
mean
low
mean
high
low
1945
1955
1965
1975
Year


(b)
Frequency
8
6
4
2
100
200
300
400
500
600
700
800
900
Rainfall (mm/yr)

Low relative humidities are characteristic of tropical arid climates. There is however, some seasonal variation related to the movements of the intertropical convergence zone (Charney, 1975) and the occurence of rain. Diurnal fluctuations inversely follow the diurnal fluctuations in temperature.

High temperatures and low humidities result in a potentially high rate of evapotranspiration. This, as well as the low unreliable rainfall, place this region in the arid ecological zone (zone VI) as designated by Pratt et al. (1966).

The climate of the Namib is more arid than that of zone VI of Pratt et al. (1976). It has been described as arid to extremely arid (Rautenbach, 1978). Arid conditions found in the Namib are caused by the combined effects of the South Atlantic anticyclone, the cold Benguela current, the upwelling of cold south Atlantic central water and the divergence of the south east trade winds along the coast (van Zinderen Bakker, 1975; Seely, 1978). The aridity of the area is furthermore accentuated by this area lying in the rain shadow of the great escarpment. All these factors combine to create a climate characterised by low rainfall (Fig. 7), fairly high humidities and a high incidence of fog near the coast (Logan, 1960; Schulze, 1969; Seely and Stuart, 1976). The mean temperature amplitude in the Namib is similar to that of the tropics (6-8°C). In winter, the easterly to south easterly hot, dry berg winds sweep off the escarpment and, in doing so, raise the temperature. In the summer months, north to north westerly winds prevail, resulting in mild temperatures with no marked seasonal fluctuations (Robinson and Seely, 1980).

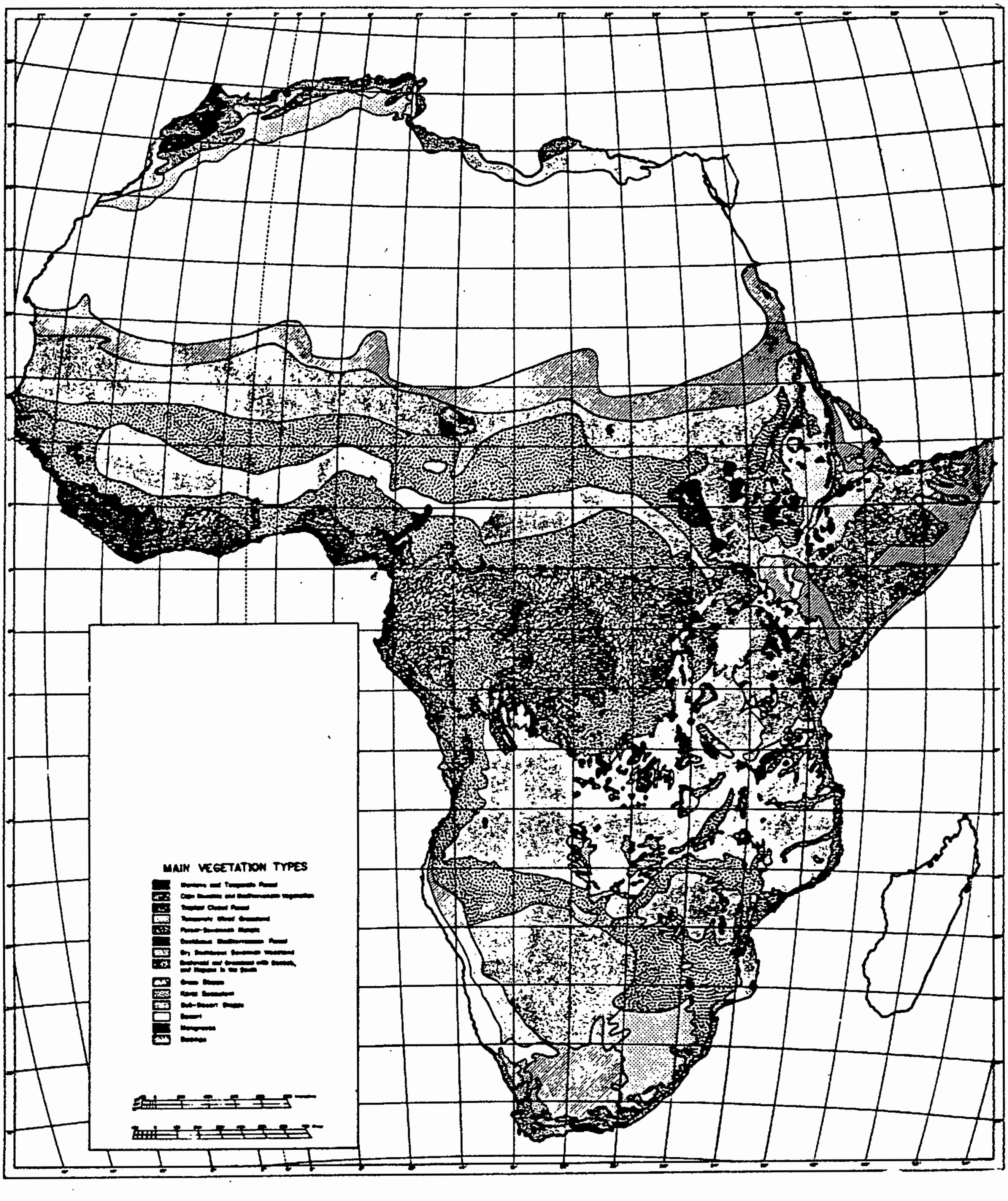
Vegetation

Gerbillus pusillus is found in the grass steppe and subdesert steppe (Fig. 9). This map is however too generalised, for tremendous vegetative differences are found in relatively small areas. These differences result primarily from the geomorphology and topography of the area and are not as distinct as the lines on the map suggest (Barkham and Rainy, 1976). There are very few published detailed accounts of the vegetation of semi-arid and arid zones of East Africa. Lind and Morrison (1974) have closely examined the grassland savanna of Tsavo (Kenya) and Barkham and Rainy (1976) have thoroughly surveyed the vegetation of the Samburu/ Isiolo (Kenya) game reserve. They found they could sub-divide this area into 18 distinct vegetation groups.

Gerbillus pusillus is found abundantly in very arid vegetation types, comprising open shrub (*Euphorbias*, *Adenium obesum*, *Cissus rotundiflora*, *Adenia venanta*, *Caralluma ruselliana*, and *Maerua crassifolia*, to mention the most common) and rare leathery xeromorphic herbs (Hubert, 1978). *Gerbillus pusillus* is also common in vegetation classified as *Acacia* desert scrub (Walter, 1971). Here the vegetation type is essentially bare and comprised of scattered stands of *Acacia nubica* and *Acacia reficiens* interspersed with short annual grasses. Ground cover here, varies considerably both seasonally and annually in response to differing amounts of annual rainfall. A lush ephemeral vegetative carpet occurs after the rains (Delany and Happold, 1979). Coe (1972) found that *G. pusillus* and two other species of gerbil were restricted to this habitat type near Lake Turkana. The more favourable riverine habitat in this region, hosted several other species.

In addition to the above mentioned vegetation types, *G. pusillus* has been recorded in the dry savanna (Dollman, 1911b; 1914b; Hubbard, 1972) and in semi-arid bushland type (Lind and Morrison, 1974). This is dominated by *Commiphora*, *Acacia*, and *Grewia*, accompanied by a variety of herbs and grasses including *Chloris*, *Zomia*, *Erogrostis* and *Panium*.

Figure 9 : Map of Africa showing the different vegetation types (from Clark, 1967)


MAIN VEGETATION TYPES

Vegetation in the three types described above, have been considerably affected by human activity (Rapp, 1974). Overgrazing by domestic herds of goats and cattle has had a profound effect on the vegetation, resulting in an exceptional increase in spiny shrubs (*Indigofera spinosa* and *Volkensinia*) and the dominance of the following grasses; *Aristida*, *Cenchrus* and *Dactyloctenium* and trees; *Acacia tortilis* and *Commiphora* species (Cloudsley Thompson, 1969). It has also been suggested that the impact of overgrazing on the vegetation, has in turn substantially reduced the amount of rainfall in the area (Charney *et al*., 1975).

There is a negligible amount of human interference in the Namib vegetation. This is primarily due to the harshness of the climate and its resulting sparse vegetation. *Aethomys namaquensis* inhabits the areas of the Namib where there is the largest diversity of perennial vegetation (Coetzee, 1969; Louw and Seely, 1982). Here fog run off and occasional rain, support a fairly rich succulent vegetation of primarily:- *Aloe dichotoma*, *Aloe namibensis*, *Euphorbia virosa*, *Commiphora sp.*, *Lithops sp.* and even the occasional *Acacia* tree. These ensure there is always some form of moisture available to this species.

The dune vegetation shows a paucity of species (Louw and Seely, 1982). Most of the vegetation occurs in the dune troughs and along the lower slopes. The main dune vegetation is *Stipagrostis sabulicola* and *Trianthema hereoensis*. Both these species are able to continue growing and flowering throughout the year, despite the absence of rain. This is facilitated through their ability to rapidly absorb moisture from fog (Seely *et al*., 1977 and Louw and Seely, 1980).

Microhabitat, social structure and activity.

The activity patterns of all mammals may be determined by a wide range of factors such as food availability, climatic conditions, nutritive demand and protection from predation. *Gerbillus pusillus* is granivorous and nocturnal, living singly in shallow superficial burrows. These burrows are approximately 20cm long ending in a sleeping chamber, approximately 15cm below the soil surface. The entrance to the burrow is plugged with sand during the day, thereby enabling the gerbil to avoid exposure to extreme temperatures, intense solar radiation, sandstorms, strong winds and day time predators. A plugged burrow invariably has a fairly high ambient humidity and facilitates the conservation of body fluids.

Although living singly (pers. obs), these rodents are gregarious, with their burrows grouped together. Social behaviour and socio-ecology in the Gerbillidae has been examined by Ågren (1979) and Daly and Daly (1975). Both these papers suggest a territorial organisation in the females and a hierarchial system in the males. This has not been investigated in either *G. pusillus* or *G. paeba*.

Gerbillurus paeba live in simple excavated burrows either in the open or more often close to clumps of dune grass. The sand in both these areas is solidified by either gemsbok urine or by fog precipitation falling from the plants (Seely, 1977). This together with the presence of plant roots, facilitates burrow construction. De Graaff and Nel (1965) studied the tunnel systems of *G. paeba* in the Kalahari and found the tunnels to be 30-40mm in diameter and 2-3m in total length, lying approximately 20cm below the soil surface. The tunnels were simple excavations with a few entrances and blind chambers in which the gerbils lived singly but in fairly close proximity to one another. The entrances are plugged with sand during the day.

The Namaqua rock rats live communally. Ten or perhaps even more rock rats utilise the same hollow nest (Smithers, 1975). Their nests are quite conspicuous and consist of grass and sticks stuffed into crevices. The entrances of these are open holes.

Reproduction

Other than litter size, little is known about reproduction in all three species. Breeding animals were found on field trips to both the Namib and northern Kenya shortly after the rains. Shortridge (1934), Christian (1979) and Withers (1983) have found breeding coincides with the rainy season. Breeding stimulation by rainfall is a common occurrence in arid environments, (Happold, 1966; Hubert, 1978; Taylor and Green, 1976), for this would coincide with the period when seeds rich in protein and energy are available (Hubert *et al.*, 1981). Loveridge (1937), whilst surveying the mammals of the rainforest region in East Africa, reported that *G. pusillus* were seasonal breeders, with a three week gestation period. He found the newborn gerbil to be blind and naked. There is some controversy as to whether the animals he described are infact *G. pusillus*, as more recent research does not extend their distribution into the rain-forests. Breeding *G. pusillus*, *G. paeba*, *A. namaquensis*, collected during this study all had relatively small litters. Only one *G. pusillus* was collected with her offspring and in that instance there were two. *Gerbillurus paeba* produced on average three to four pups and *A. namaquensis* had litters of three to five young. Smithers (1971) reported litters of up to seven young. Both *G. paeba* and *A. namaquensis* bred in captivity. The young of the latter cling resiliently to the mammae while the mother moves around whereas the offspring of *G. paeba* normally remained in the nest while their mothers were out of the nest.

Diet and Predation

Mathur and Prakash (1980) found a greater readiness in rodents from arid areas to sample new foods, albeit in small quantities for the first few days, than rodents from areas where food supply is more or less continuous throughout the year. It is hardly suprising then that the diet of these three African rodents is primarily granivorous but also generalistic, supplemented with leaf, stem and insects when available (Jarvis pers com., Buffenstein, 1977; Christian, 1979; Wassif and Soliman, 1979; Withers, 1979). Several species are known to hoard caches of food in their burrows (Happold, 1968; Christian *et al*., 1977; Pettifer and Nel, 1977; Wassif and Soliman, 1979). This was certainly true for G. paeba, but not for A. namaquenis and it is not certain whether G. pusillus conforms to this trend.

Petter (1961) found well worn paths running from the burrows to the feeding areas in G. pusillus. They tend to forage close to cover so as to avoid detection by predators (Kingdom, 1974) and this seemed to hold true for the Namib species examined. Virtually nothing is known of the predators of these rodents. Silver jackal have been observed interfering with traps; however it is probable that most of the abundant small carnivors, snakes and raptors prey upon these animals (Coetzee, 1969; Stuart, 1975; Delany and Happold, 1979).

Limited studies have been conducted on the two Namib species. Christian (1979; 1981) has examined the demography of G. paeba. Included in those studies are some data on their reproduction and water requirements. Withers (1979) conducted a year long population study of the rodents on the inselberg at Tumasberg. This provided much information about the microhabitat of Aethomys, its population stability (Withers, 1979) and its reproductive cycle (Withers, 1979; 1983). In addition he also examined their daily water turnovers and daily energy expenditure (Withers et al., 1980). Besides these studies little is known about these animals. Aside from the taxonomic studies and scant references to habitat and reproduction of G. pusillus normally incorporated in listings of rodents from various areas, nothing is known about the ecology and physiology of this nocturnal granivore.

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PART 2

CHAPTER 2

Thermoregulation and metabolism in the smallest African gerbil, *Gerbillus pusillus*.

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Running title: Thermoregulation in *Gerbillus pusillus*.

Synopsis

The effect of temperature on thermoregulation, metabolism, evaporative water loss and thermal conductance was studied in Gerbillus pusillus. Its resting body temperature (TB) was 34.6 °C, approximately 5 °C higher than the mean ambient temperature (TA) encountered in its burrow. As TA increased above 34 °C, its ability to lose heat to the environment decreased. It overcame this problem by tolerating increases in TB to a non-lethal maximum of 41 °C, whilst also eliminating increasing quantities of obligate heat by pulmocutaneous evaporation and conduction.

Metabolic rate was 41% lower than that predicted from Kleiber's (1975) allometric equation. This confers a considerable saving in energy in an environment where food is often scarce, whilst simultaneously reducing heat production and the degree of gaseous exchange in the already oxygen poor and carbon dioxide rich environment encountered in the plugged burrows of its natural milieu.

Gerbillus pusillus therefore does not maintain strict homeothermy and utilizes a labile TB and reduced metabolic rate as an adaptive mechanism for survival in the arid zones of tropical Africa.

Contents

Introduction

The smallest African gerbil, *Gerbillus pusillus*, weighing approximately 13g, is found in the drier regions of Eastern Africa. Despite its abundance, little is known of its ecology other than that it is found in shallow burrows (approximately 15cm deep) on open alluvial flats (Coe, 1972) and in open scrub savanna (Hubert, 1978). Here high soil surface temperatures, low humidites and sparse vegetation render the area a most unsuitable terrain for small mammals.

Because of their small size and thermal sensitivity, rodents have made maximum use of burrows to avoid exposure to hostile environments (Kirmiz, 1962; Schmidt-Nielsen, 1975; Louw and Seely, 1982). However, this 'escapism' is insufficient to insulate them completely from the stresses of their milieu and has led to a great diversity of thermoregulatory responses to climate including: hibernation (Bartholomew and MacMillen, 1961; Bradley *et al*., 1975), aestivation (Hudson and Bartholomew, 1964; Hill, 1975; Hudson and Scott, 1979) and other physiological responses (Gorecki, 1968; Jansky *et al*., 1969; Hainsworth and Strickler, 1969). All these studies have underlined the importance of considering the microclimate in which the rodent lives, in relation to its physiology.

Inhabitants of closed burrow systems are exposed to very different environmental conditions when compared to other terrestrial mammals: light, temperature and humidity are relatively constant (Schmidt-Nielsen *et al.*, 1970; Baudinette, 1972; Arieli *et al.*, 1977). Oxygen levels are lower and carbon dioxide levels are higher than atmospheric (Darden, 1972; Kay, 1975). Burrow humidities are high, thereby limiting the avenues for effective heat exchange through evaporative water loss. Convection currents in the plugged burrow are also impeded and limit effective heat exchange from the animal by conduction and radiation.

This paper examines the metabolic and thermoregulatory adaptations in *G. pusillus* to determine how this animal overcomes the thermal problems encountered in its milieu and whether its thermoregulatory adaptations are consistent with those of other rodents (Hart, 1971) inhabiting harsh arid environments.

Procedure

Maintenance

For two months prior to the experiment, a pool of fifteen G. pusillus (collected in northern Kenya; 0°38'N, 37°47'E) were kept individually in glass terraria floored with fine sand and containing a nest box. The terraria were placed in an air conditioned room with a 12L:12D photoperiod at a temperature of 22-26 °C and a relative humidity of 44-50%.

The gerbils were fed an ad lib. diet of mixed bird seed. Water was provided in the form of fresh vegetables. During this period body mass was regularly monitored to the nearest 0.1g using a Mettler portable balance.

Experimentation

The effect of ambient temperature (TA) on body temperature (TB), oxygen consumption and evaporative water loss were monitored together in twelve gerbils. This was done during daylight hours (8.00h - 17.00h) when the gerbils are normally inactive.

Body temperature

Diurnal changes in TB at a constant TA of 22 - 26°C were monitored between 7am and 2am. A copperconstantan thermocouple was inserted approximately 1cm into the rectum at two hourly intervals. The thermocouple was connected to a calibrated digital display (Bailey Bat).

The relationship between TB and TA (12 - 41°C) was monitored in twelve gerbils. The gerbils were given four hours to become thermally equilibrated before TB was recorded. At TA above 40°C, this equilibration period was reduced to 2.5 hours. All measurements were taken immediately after monitoring oxygen consumption and evaporative water loss.

Oxygen consumption

Oxygen consumption (VO_2) and evaporative water loss (EWL) of twelve gerbils were measured simultaneously over TA 12 - 41°C. This was done by placing a non-fasting post absorptive gerbil (i.e. one that had eaten during the scotophase, but had stopped eating at least four hours prior to the commencement of the experiment), in a clear perspex chamber (75mm by 150mm) with a wire mesh platform on which the rodent rested. The chamber and a similar one without an animal (the control) were placed in a larger constant temperature and humidity chamber (TA control ± 1.0°C, humidity control ± 2.0%). Each chamber was equipped with ports for a thermocouple and air vents. Air at 50% humidity flowed through the chamber at 132 $cm^3.min^{-1}$ and then over a relative humidity probe (Vaisala humicap HM1-14) before being dried over silica gel and fed into an oxygen analyser (S-3A, oxygen analyser, N-37 oxygen sensor, Applied Electrochemistry Inc.). The oxygen analyser monitored the difference in oxygen content between the two chambers. The oxygen analyser, temperature thermocouples and relative humidity probe were connected to a data logger (Esterline Angus P.D. 2064) which was programmed to record at five minute intervals.

At each new TA the animal was allowed to equilibrate for one hour. Thereafter, VO_2 was monitored for at least three hours. At each TA, the lowest six readings for each animal, corrected to STP, were used in calculating the post absorptive resting minimal metabolic rate. Rectal temperatures were taken at the end of each run.

Evaporative water loss

Evaporative water loss was determined from the change in relative humidity between the air leaving the experimental chamber and the control using the equation:

$$WL = \frac{CTA \times \text{©}RH \times F \times 60}{1000 \times 100 \times M}$$

where WL is water loss (mg H O. g.$^{-1}$h^{-1}), CTA is mass of water in saturated air at TA (g.m^{-3}), ©RH is the change (%) in relative humidity caused by the animal, F is the flow rate (cm^{3}.min^{-1}), and M is mass of the animal (g).

So as to avoid damage to the oxygen sensor no mineral oil was placed beneath the mesh in the chamber. During the experimental run, the chamber was frequently examined through a viewing port in the outer temperature control chamber. If the gerbil had roused and urinated, the run was interrupted, the apparatus cleaned and dried and left to equilibrate for 20 minutes. As most gerbils urinated on handling, prior to being placed in the chamber, such interruptions were infrequent.

Thermal conductance

'Conductance is the rate of dry heat transfer (i.e. excluding evaporative water loss) per unit area to or from the animal per degree temperature difference between the animal and its environment' (Dawson and Schmidt-Nielsen, 1966, p. 466).

Mean conductance (Cd) between the body core and its environment was measured by the simultaneous measurement of metabolic heat, heat dissipated by EWL and the difference between TB and TA, using the equation:

$$Cd = \frac{HP - EHL}{T \times S} \quad \text{(Dawson and Schmidt-Nielsen, 1966)}$$

where Cd is dry thermal conductance ($J.cm.^{-2}\ ^{\circ}C.^{-1}h^{-1}$), HP is metabolic heat production ($J.h^{-1}$) assuming 1 cm^3 oxygen is equivalent to 20.1J, EHL is evaporative heat loss ($J.h^{-1}$) assuming 1mg water is equivalent to 2.34J, T is (TB - TA, °C), S is surface area of a mouse (cm^2) where $S = 10 \times mass^{0.67}(g)$.

Thermal conductance, measured this way, shows the capacity (summating all the individual characteristics e.g. vaso-constriction, pilo-erection, posture, etc.) of the animal concerned, for heat loss through conduction, convection and radiation.

Minimal conductance

Minimal conductance (i.e. including evaporative water loss) is calculated from the equation:

$$Cm = \frac{M}{TB - TA} \qquad \text{(McNab, 1980)}$$

where Cm is the minimal conductance ($cm^3O_2 .g.^{-1}\ {}^{\circ}C.^{-1}\ h^{-1}$) and M is the resting metabolic rate ($cm^3O_2 . g.^{-1}h^{-1}$).

Minimal conductance was also calculated from the slope of the graph relating VO_2 with TA, below the region of thermoneutrality, using McNab's (1980) correction factor.

Unless otherwise stated, means and standard errors are given with the number of observations in brackets.

Results

Body temperature

A diurnal cycle in TB was apparent at TA 22 - 26 °C. The TB during the day was fairly stable ranging between 33.6 °C and 36.9 °C (mean TB 34.69 ± 0.12 °C; n = 45). In the evening, TB was higher ranging between 35.7 °C - 37.2 °C with a mean of 36.25 ± 0.08 °C, n = 30). The TB of G. pusillus was fairly stable over a TA range of 12 °C to 34 °C. At these TAs, TB of G. pusillus ranged between 33.5 °C- 36.9 °C with an average TB of 34.64 ± 0.12 °C (n = 70), indicated in Fig. 1 by the line AB.

Above TA 34 °C the gerbils became hyperthermic TB rising with TA (as shown by the line BC in Fig. 1) in accordance with the equation:

$$TB(^{\circ}C) = 14.3 + 0.6\ TA(^{\circ}C) \quad r = 0.93\ (n = 54)$$

Two animals died after exposure to TA 41 °C for two hours. The lowest experimental temperature used (TA 12.0 °C) did not induce hypothermia.

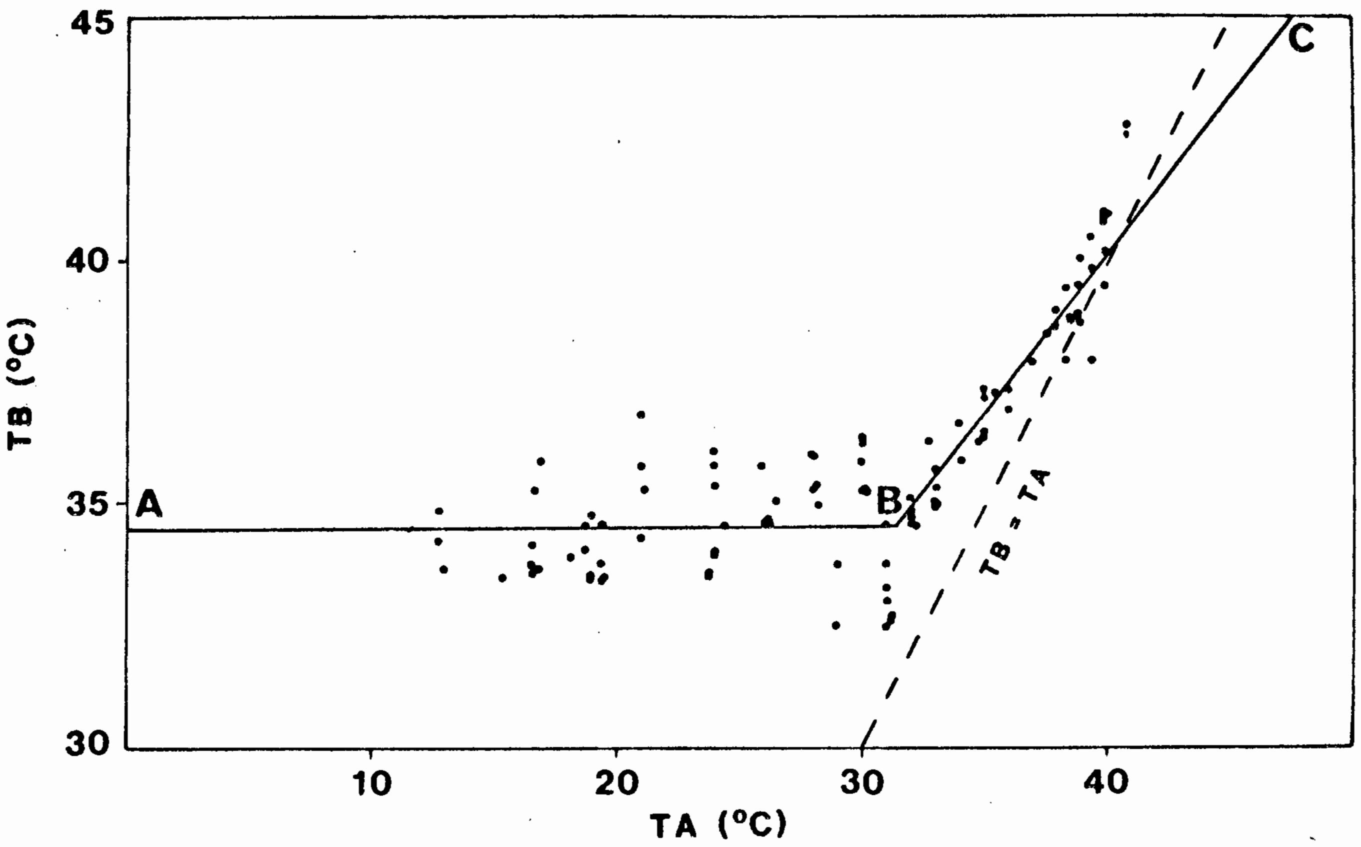

Figure 1 : Effects of ambient temperatures (TA) on body temperature (TB) in *Gerbillus pusillus*

Oxygen consumption

Rates of oxygen consumption for males (n=6) and females (n=6) showed no significant difference at all experimental TAs ($p \geq 0.10$). Data were therefore combined.

Between TA 12 °C and 31.4 °C, VO_2 decreased linearly (as shown by the line AB in Fig. 2) with increasing TA according to the equation:

$$VO_2 (cm^3 O_2 .g.^{-1} h^{-1}) = 7.75 - 0.21TA(°C) \quad r=0.95 \; (n=72)$$

Extrapolation of this line intersects the abscissa at TA 36.33 °C. This is 1.69 °C higher than the resting TB but is the same temperature as the mean TB recorded at night when the animals are active. The intercept value of 7.75 $cm^3 O_2 .g^{-1} h^{-1}$ at TA 0 °C was found to be approximately seven times the minimal metabolic rate.

Between 31.4 and 38 °C, oxygen consumption was minimal and constant (mean 1.07 ± 0.03 $cm^3 O_2 .g^{-1} h^{-1}$, n = 37; as shown by the line BC in Fig. 2). These temperatures were the limits of the zone of thermoneutrality.

Above the upper limit of thermoneutrality (38 °C), VO_2 again increased linearly with TA (as shown by the line CD) according to the equation:

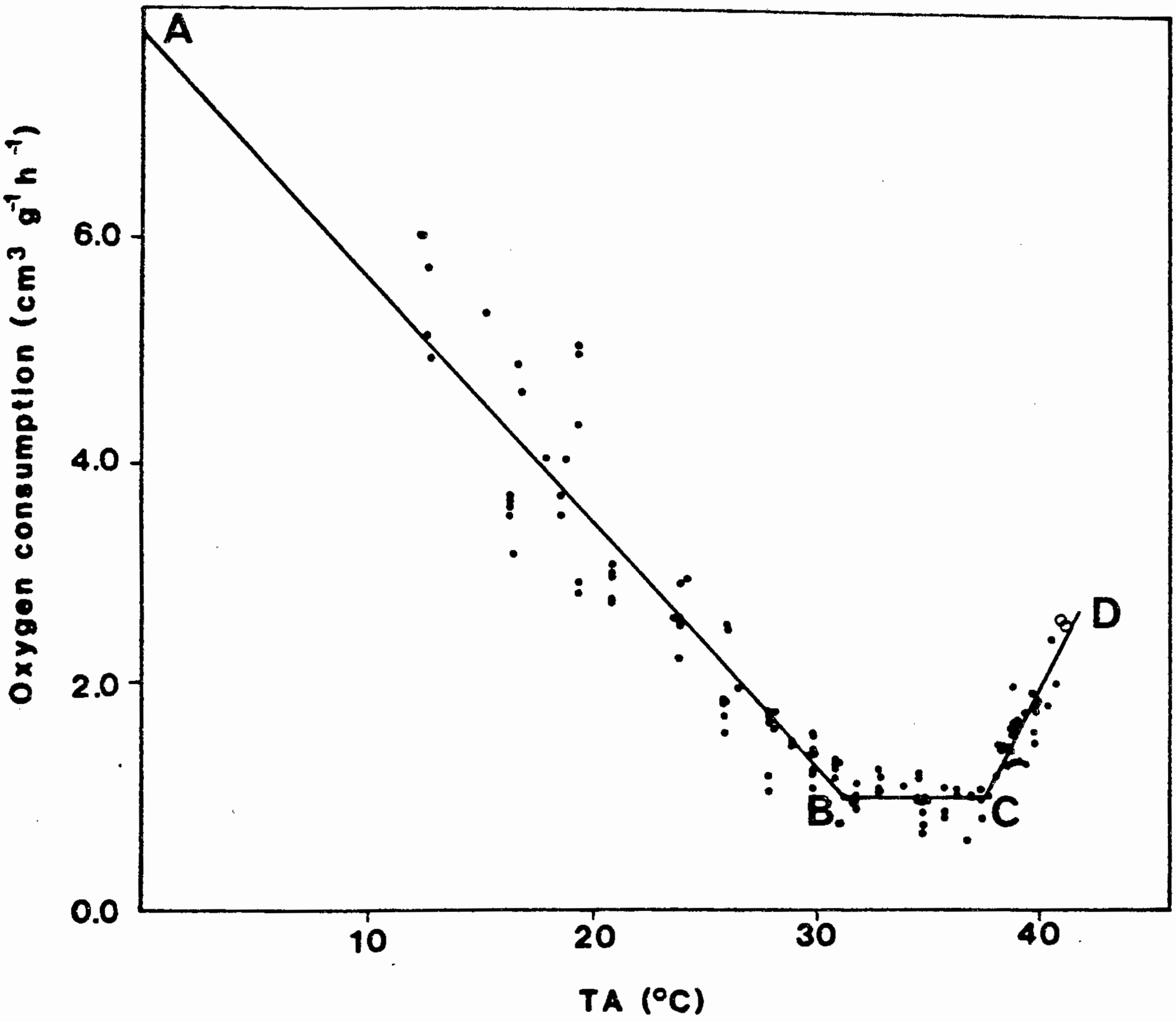

Figure 2 : Effects of ambient temperature (TA) on oxygen consumption in *Gerbillus pusillus*

$$VO_2\ (cm^3 O_2 .g^{-1}h^{-1}) = -14.49 + 0.41TA(°C)\ r=0.88\ (n=36)$$

Evaporative water loss

In the comparatively dry air of the experimental chamber, at TAs between 12 and 38.5 °C, the mean rate of EWL remained fairly stable at 2.43 ± 0.07 mg $H_2O.\ g^{-1}h.^{-1}$. Evaporative water loss began increasing at the upper critical limit of the TNZ and reached a maximum of 13.82 mg $H_2O.\ g.^{-1}h^{-1}$ at 41 °C, the lethal TA.

The ratio EWL/VO_2 increased with increasing TA (Fig. 3) from a low of 0.49 ± 0.04mg $H_2O.\ ml^{-1}O_2$ (n = 12) below 17 °C to a maximum of 1.83 ± 0.08mg $H_2O.\ ml^{-1}O_2$ (n = 13) at 31.5 °C. Above this temperature, water loss increased rapidly and individual variation was marked. This high water loss was probably due to excessive salivation at these temperatures.

Energy values of 2.34J.mg $^{-1}$ water and 20.1J.cm^3 oxygen were used in converting EWL and VO_2 to thermal units. The proportion of metabolic heat lost through evaporation was a maximum at the lethal temperature when 62.8% of the heat produced was removed through water loss (Fig. 3).

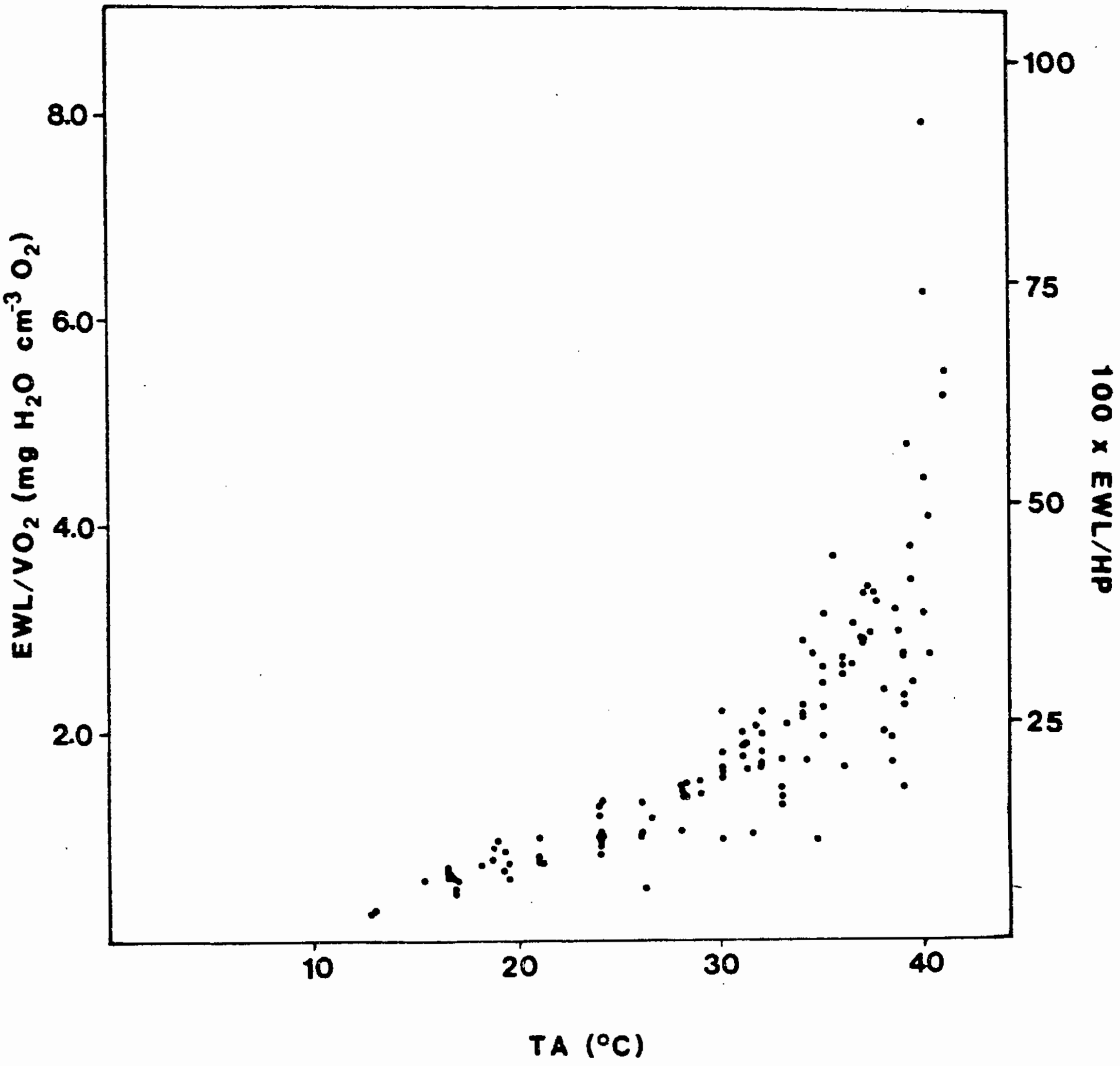

Figure 3 : The effect of ambient temperature (TA) on i) (left hand ordinate) the ratios of evaporative water loss (EWL) to simultaneous oxygen consumption (VO_2) and ii) (right hand ordinate) evaporative heat loss as a percentage of metabolic heat production (HP) in *Gerbillus pusillus*. Values of 2.34 $J.mg^{-1}H_2O$ and 20.1 $J.cm^{-3}O_2$ were used to convert EWL and VO_2 to thermal units.

Thermal conductance

Below TA = 30 °C, Cd remained relatively constant with a mean value of 1.00 ± 0.21 $J.cm^{-2}..°C.^{-1}h^{-1}$ (n = 50). Under these conditions, Cd was minimal and insulation maximal. As the differences between TA and TB decreased (Fig. 4), the Cd increased becoming maximal when TB - TA approached zero (Fig. 4). In five instances at high TA, Cd values were negative. Here TB was less than TA, suggesting a reversal of heat flow from the environment to the animal and that these gerbils were capable of physically maintaining their TB below TA. Calculation of Cd becomes increasingly uncertain as the difference between TB and TA approaches zero. Firstly any error in the measurement of TB becomes increasingly important. Secondly, because the animals become more restless, the surface area assumed to be constant, might change.

Minimal conductance

Because few studies have monitored oxygen consumption and evaporative water loss simultaneously (Herreid and Kessel, 1967), wet or minimal conductance (Cm) was calculated for comparative purposes. At temperatures below TA 28 °C Cm values were stable. The resulting Cm mean was 0.24 ± 0.04 (n = 36) $cm^3O_2.g^{-1}.°C.^{-1}h.^{-1}$.

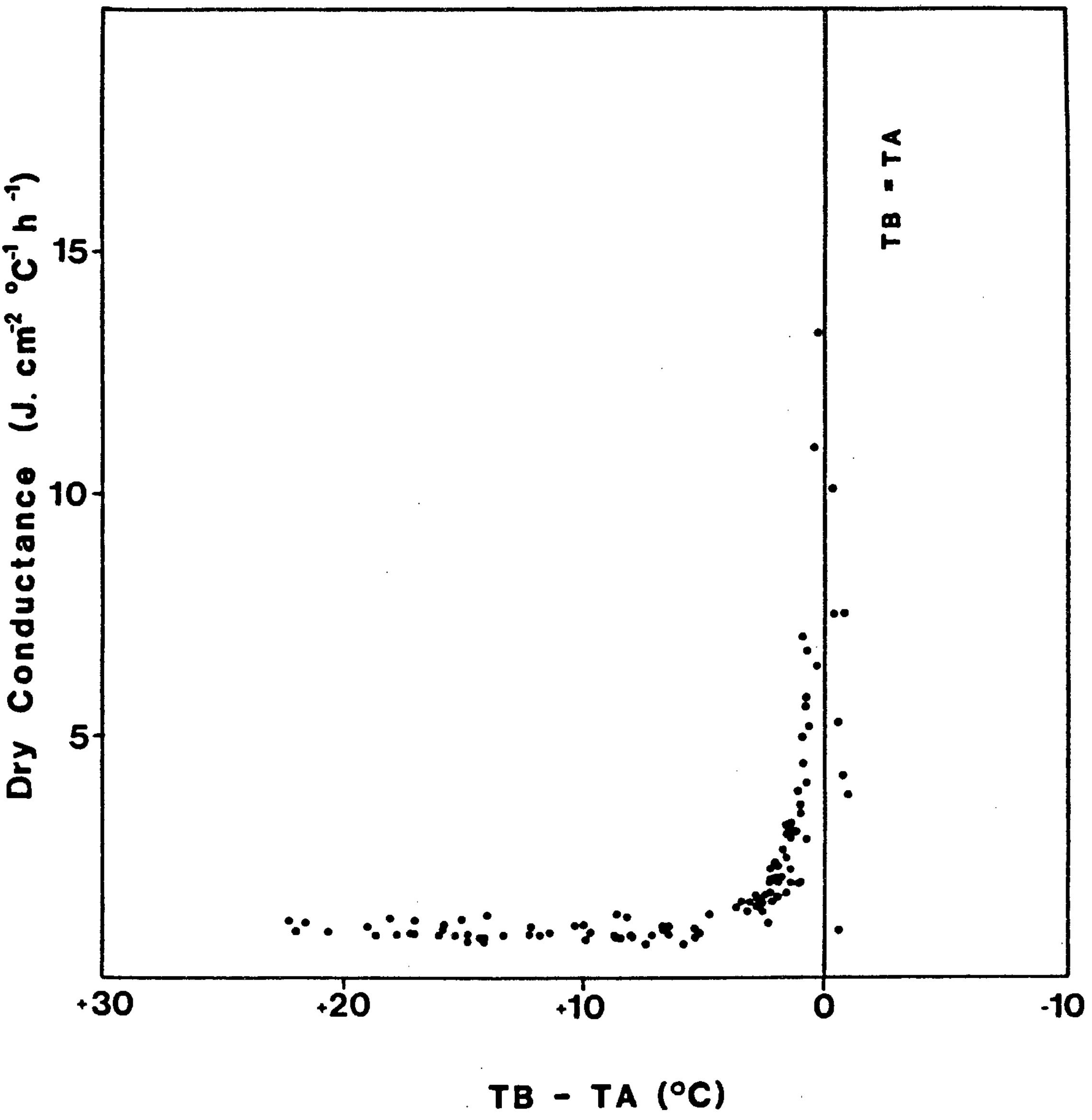

Figure 4 : Thermal conductance (Cd) of *Gerbillus pusillus* in relation to the difference between body and ambient temperature (TB - TA)

These results were compared with the Cm obtained from the slope of the equation linking VO_2 and TA, using McNab's (1980) correction factor. This corrected Cm was similar to that measured 0.23 $cm^3O_2 .g^{-1} . °C.^{-1}h.^{-1}$. Above 28 °C G. pusillus used behavioural means (eg. posture) as well as vasomotor control to increase conductance.

Behavioural responses to changes in temperature

When measuring non-restrained metabolic rates and body temperatures, a certain amount of activity always takes place. This cannot be easily separated from the influence of environmental temperature on thermoregulation. The gerbils were least active in the TNZ and changed their resting posture from a crouched upright position to lying on their sides, abdomen or back, with limbs outstretched. Above the TNZ, G. pusillus became restless having short bursts of frantic activity interposed with periods of calm, lying in an outstretched position. Licking of front limbs and salivation was observed above the TNZ, this became more pronounced with increasing temperature.

Discussion

Body temperature and microhabitat

Gerbillus pusillus live in superficial burrows approximately 15cm deep (pers. obs.). In northern Kenya in August 1980, average burrow temperatures 9 and 19cm below the soil surface showed a diel range of 26.6-35.7 °C and 28.2-32.5 °C respectively, with a mean of 30.0 ± 1.3 °C. During the same period, soil surface temperatures ranged from 25-63 °C (Jarvis unpubl. data). Seasonal soil temperature fluctuations would most probably be small as the annual amplitude in air temperature ranges between 2-6 °C (Gorou, 1970). It therefore appears that burrow temperatures normally encountered by resting gerbils are slightly lower than the lower limit of thermoneutrality (31.4 °C). At these temperatures, only slight energy expenditure is required to maintain TB at the resting mean value and thermal stress is not encountered in the plugged burrow even when soil surface temperatures are at a maximum. The resting TB (34.6 °C) of *G. pusillus* is lower than that expected for homeotherms (Swan, 1974). Contrary to the findings of Scholander *et al.* (1950), there appears to be a general tendency for decreased TB in small mammals in desert climates (Table 1). *Gerbillus pusillus*' TB is still lower than that of most

TABLE 1 Energy metabolism and thermoregulation in some rodents from arid and mesic environments

	Mass	BMR^{+}		C_m^{++}		F"	TB	TNZ		TA_L	Source
	(g)	$\bar{x}$	%$^{\neq}$	$\bar{x}$	%$^{\neq\neq}$		°C	L °C	U °C	°C	
ARID											
*Perognathus longimembris**	8.9	1.07	54	0.28	84	0.64	35	30	-	-	Chew *et al.* (1967)
Leggadina hermannsburgensis	12.2	1.91	104	0.30	108	0.97	38	31	36	>37	MacMillen *et al.* (1972)
*Gerbillus pusillus**	12.6	1.05	58	0.24	89	0.65	35	32	38	41	Present study
Perognathus intermedius	15.2	1.32	76	0.24	97	0.78	35	33	36	40	Bradley *et al.* (1975)
*Peromyscus eremicus** (New Mexico)	20.0	1.32	82	0.19	88	0.93	36	30	36	>39	McNab & Morrison (1963)
*Perognathus californicus**	22.0	0.97	61	0.19	89	0.69	38	33	33	37	Tucker (1965)
*Peromyscus truei**	33.0	1.53	109	0.13	84	1.29	37	29	35	-	McNab & Morrison (1963) & Carpenter (1966)
Notomys cervinus	34.0	1.22	86	0.19	113	0.76	-	33	33	-	MacMillen & Lee (1970)
Dipodomys merriami	38.0	1.13	82	0.11	68	1.21	37	32	35	40	Carpenter (1966)
Liomys salvani	44.0	1.07	81	0.19	126	0.64	37	31	34	36	Hudson & Rummel (1966)
Jaculus deserti	106.0	0.87	82	0.08	88	0.93	37	28	35	-	McNab (1979)
Dipodomys deserti	75.0	1.23	106	0.13	119	0.89	37	33	35	-	McNab (1979)
Jaculus orientalis	139.0	1.00	100	0.08	102	0.98	37	28	33	>40	Hooper & Hilali (1972)
MESIC											
Reithrodontomys megalotis	9.0	2.50	127	0.27	83	1.53	37	33	35	37	Pearson (1960)
Ochrotomys nuttali	20.0	1.39	85	0.21	98	0.87	36	30	36	-	Layne & Dolan (1975)
Napaeozapus insignis	22.0	1.80	114	0.27	132	1.15	37	30	34	37	Brower & Cade (1966)
Akodon azarae	25.0	1.70	111	0.23	120	0.92	35	30	32	37	Dalby & Heath (1976)
Peromyscus truei gilberti	33.0	1.90	133	0.14	84	1.58	37	27	33	-	McNab & Morrison (1963)
Mus musculus	46.0	1.47	112	0.15	107	1.05	37	27	33	38	Hudson & Scott (1979)
Dipodomys agilis	61.0	1.05	86	0.08	64	1.35	37	26	36	-	Carpenter (1966)
Peromyscus thomasi	111.0	1.12	106	0.07	79	1.34	38	28	35	-	Musser & Shoemaker (1965)
Rattus norvegicus	160.0	1.31	126	0.09	123	1.02	37	25	31	40	Kirmiz (1962)

$^{+}$ BMR = $cm^3 O_2 . g^{-1} h^{-1}$

$^{++}$ C_m = $cm^3 O_2 . g^{-1} \cdot C^{-1} h^{-1}$

$^{\neq}$ M_B(%) = $100 . BMR / (3.42 . W^{-0.25})$, Kleiber (1975

$^{\neq\neq}$ C_m(%) = $100 . C_m / (1.02 . W^{-0.519})$, Aschoff (1981)

" F = M_B(%)/C_m(%), McNab (1979)

* Species known to employ torpor

arid-adapted rodents. From a standpoint of conserving energy, it is most expedient for arid-adapted homeotherms to have a resting TB close to the effective TA. Insulation by morphological and behavioural means, rather than metabolic expenditure, would then allow the TB to remain at the desired level.

Temperature regulation

Between TA 12 and 34°C, resting TBs were independent of TA (Fig. 1). However, at TAs above 34°C, TB of resting gerbils increased but at a lower rate than ambient. Many desert rodents (e.g. *Peromyscus maniculatus*) show similar response to elevated TA (Hart, 1971). As TA increases, *G. pusillus*, like other rodents, is faced with the potential problem of a decreased ability to lose heat to its environment. It overcame this problem by tolerating increases in TB, whilst also eliminating some heat by evaporative water loss and conduction. Hyperthermia commenced within the TNZ and substantial quantities of heat were stored (Fig. 5) before there was a noticeable increase in oxygen consumption. This phenomenon is not uncommon in desert rodents. It is however, most pronounced in larger diurnal rodents e.g. *Spermophilus leucurus*, *Citellus leucurus* (Hudson, 1962), but also frequently occurs in nocturnal rodents e.g. *Acomys cahirinus* (Shkolnik and Borut, 1969) *Dipus*

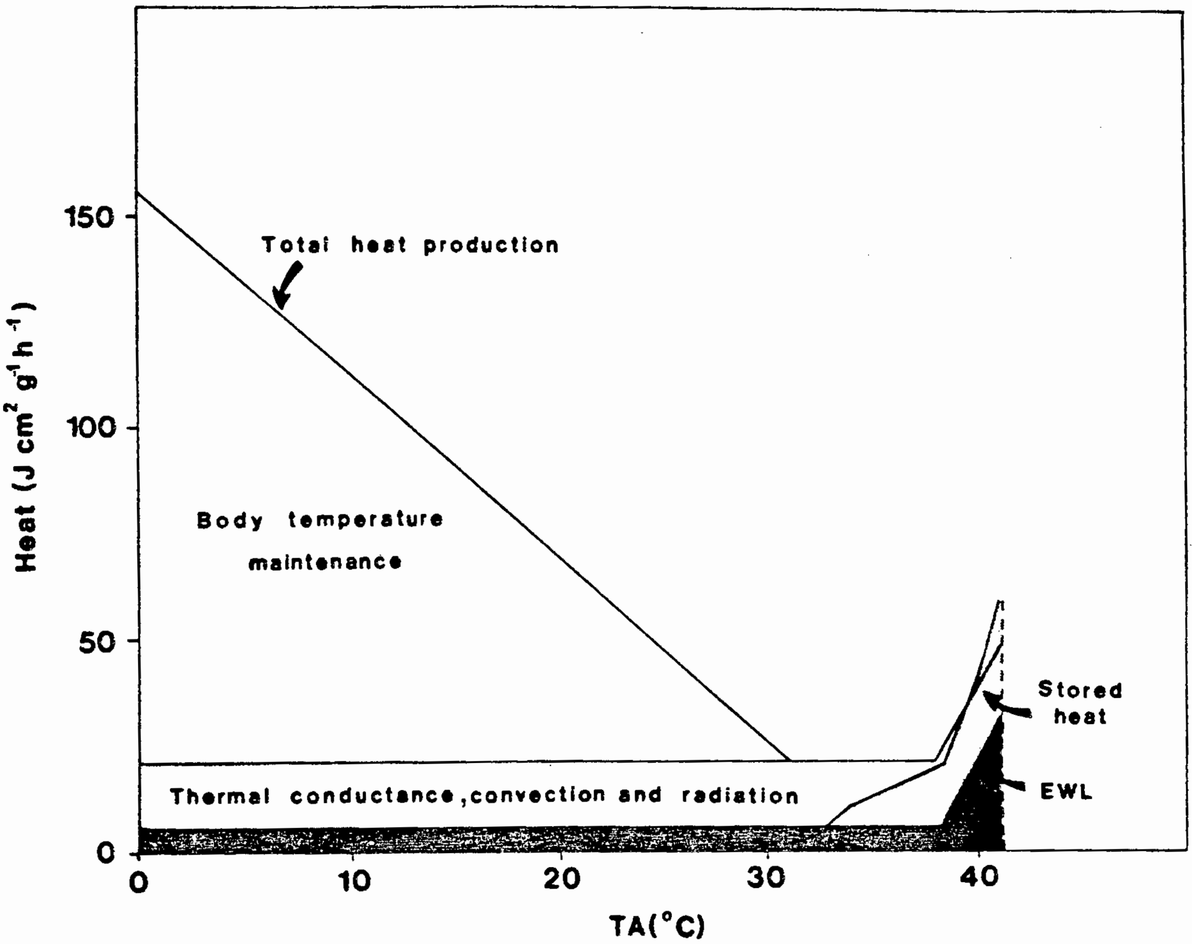

Figure 5 : The effect of ambient temperature (TA) on the proportion of heat produced, dissipated and stored in *Gerbillus pusillus*. All values were calculated from oxygen consumption and evaporative water loss. The calculations assumed 1 mℓ of oxygen when used in oxidative metabolism yields 20.46 kJ. Latent heat of vaporization was taken as 2.426 kJ.g^{-1} water. Specific heat capacity of mammalian tissue is 3.431 J.g^{-1}.°C^{-1}.

aegiptus (Kirmiz, 1962), Notomys alexis (MacMillen and Lee, 1970), and Rattus villosimus (Collins and Bradshaw, 1973). This tolerance to hyperthermia with avoidance of hypermetabolism tends to decrease hyperthermia itself, as well as the amount of evaporative cooling. As G. pusillus is small, the benefits of hyperthermia, being related to the thermal inertia of the animal, would be far less than that of an animal with a larger body mass.

Because of the variation of the methods used, much difficulty arises when evaluating and comparing the degree of tolerance to hyperthermia and the lethal temperatures of rodents. Several factors should be taken into account, namely:(a) the type of measuring device used, (b) where the temperature was measured, (c) how deep the thermometer was inserted, (d) duration of exposure to any TA, (e) the ambient humidity, (f) availability of water, (g) previous thermal history. With much reservation then, it appears that G. pusillus can tolerate higher TA's (up to 40°C) than most of the desert rodents mentioned in the literature (e.g. Hart, 1971), an exception being Spermophilus leucurus (Hudson, 1962). Gerbillus pusillus' tolerance of high temperatures can possibly be explained by the warm microhabitat it inhabits, where burrow temperatures are higher than those recorded for most rodents (Kennerly, 1964; McNab, 1966). Acclimation to high temperatures could confer greater tolerance to increased TAs.

Oxygen consumption

The basal metabolic rate (BMR) of G. pusillus was 58.8% of that predicted allometrically from Kleiber's (1975) equation for euthermic metabolism. This deviation is not uncommon in desert rodents (Table 1) and supports the concept that a lowered metabolism is an adaptive mechanism for reducing heat and water expenditure, factors of prime importance for successful living in harsh arid environments (Bradley and Yousef, 1972).

The microclimate within the burrow imposes energetic constraints on fossorial and semifossorial rodents. These problems are pronounced in sleeping G. pusillus, in that the burrow system is merely an excavated nest, maintained at temperatures slightly lower than the lower critical limit. This problem is compounded still farther by the gerbil blocking the entrance and thus minimising ventilation and heat loss by convection, conduction and radiation. Humidities in the burrow, although not measured in this investigation, are generally high and are expected to be similar to those measured in gopher burrows (Kennerly, 1964; Darden, 1972), precluding heat loss by evaporative cooling. In this milieu, a lowered BMR is advantageous, reducing the degree of gaseous exchange in an already oxygen poor and carbon dioxide rich environment and decreasing the heat load in the burrow. Heat loss under these conditions is enhanced by hyperthermia producing a positive heat differential gradient between the animal and its' environment. Lowered heat production associated with a reduced metabolic rate not only conserves energy but simultaneously decreases respiratory water loss and therefore confers another though secondary advantage. Peculiarly, *Leggadina hermansburgensis*, a most successful Australian desert rodent, has a metabolic rate in close agreement with the predicted value for an animal its size (MacMillen *et al.*, 1972) as does *Jaculus deserti* a north African dipodomid (Hooper and Hilali, 1972). By extrapolating data from these species and several others, McNab (1979) concluded that successful desert dwelling rodents that did not exhibit reduced BMR compensated for the increased water loss by producing exceptionally concentrated urine. *Gerbillus pusillus* is a successful desert rodent, in that it can survive indefinitely on a diet of air dried seed in the laboratory. It conforms to McNab's (1979) findings in that water savings from its reduced BMR are balanced by the excretion of a moderately concentrated urine (approximately, 4000mOsm.kg $^{-1}$; Buffenstein, in prep a).

Low BMRs, whilst providing a means of balancing water loss in xerophilic rodents are also advantageous in balancing the daily energy requirements. Also, as the position of the lower critical temperature is governed by the rate of change in VO_2 and TA, it follows that a reduced BMR will result in an elevated lower critical temperature. This will enable G. pusillus to enter torpor (Buffenstein, in prep b) at relatively high TAs.

Evaporative water loss

Below thermoneutrality EWL is essentially independent of TA (Fig. 3). It increased 1.5 times between the two limits of the TNZ and was found to be associated with the onset of hyperthermia. At the upper critical temperature 29% of the heat produced was lost via evaporative cooling (Fig. 3) and this increased to 63% at TAs close to the lethal temperature (41 °C).

At TAs above the TNZ, G pusillus salivates, licking its forelimbs. Whilst these gerbils lose a considerable quantity of water through 'insensible perspiration', it is most probable that much of the measured EWL at high TAs resulted from salivation. Despite this additional behavioural mechanism to increase heat loss, the total heat load was not dissipated, resulting in an increased TB (Fig. 5). Most research on arid-adapted rodents (with the exception of Spermophilus richardsonii, Hudson and Deavers, 1973) indicates that rodents are not capable of dissipating metabolic heat solely through evaporative cooling (Wunder, 1970). Use of salivation to increase evaporative cooling is fairly widespread throughout the mammals (Bligh, 1976). It is however merely used as a short term emergency regulation when TB approaches lethal levels, for water resources in small animals are insufficient for long term use in heat regulation.

The magnitude of pulmocutaneous water loss depends primarily on TA, relative humidity and expired air temperature. The importance of humidity was emphasised by Baudinette (1972), Edwards and Haines (1978) and Withers _et al_. (1979). They have demonstrated that rodents kept in moist air became hyperthermic whereas those maintained in dry air showed only slight increases in TB. Absolute humidity in the chamber is governed by the combined effects of flow rate, incurrent humidity and EWL. Because it is therefore impractical to create a specific hygric environment in a metabolic chamber (Welch, 1980), comparisons of evaporative water losses recorded in the literature should be treated with caution, for these often merely reflect differences in experimental technique. The EWL values for _G. pusillus_ were nevertheless mid-range.

Thermal conductance

The parameters TB, BMR and the rate of EWL are easily measured. Thermal conductance on the other hand, is indirectly measured from the three parameters discussed above, together with air temperature and body mass. Its extrapolation rather than direct measurement and its non-uniformity have resulted in a widespread conceptual misunderstanding of its meaning (McNab, 1980).

Thermal conductance is the measure of the ease with which heat enters or leaves the body. However, it is a highly complex interaction of environmental factors with physiological and anatomical features such as fur thickness, pilo-erection, subcutaneous fat deposition and vasomotor changes (Herreid and Kessel, 1967). Conductance, or its reciprocal insulation, is extremely important in a small mammal for, (i) conductance through the body core to the skin surfaces is high as a result of the high rate of heat transfer through tissues and the small distances involved (ii) there is a large surface area / volume ratio through which heat is lost to the environment (Dawson and Dawson, 1982). _Gerbillus pusillus_ employs the same physiological mechanisms normally used by mammals for the maintenance of homeothermy both at high and low TAs. At TA 12 °C, the lowest TA measured in this investigation, metabolic rate increased approximately five-fold above the minimal level. Thermal conductance below 30 °C remained relatively constant suggesting that at moderate temperatures, physical thermoregulation (conductance) plays a minor role in thermoregulation and is inadequate for maintaining a steady temperature. The same situation is true of most small mammals (Bradley and Deavers, 1980). As TA approached TB, there was a marked increase in conductance (Fig. 4) so facilitating heat loss and economising on water loss. Conductance, together with hyperthermia, results in a saving in water that otherwise would have been required for evaporative cooling.

Aschoff (1981) stressed the influence of circadian phase on minimal conductance and showed conclusively that previous equations relating minimal conductance to body mass were incorrect, because data used in their calculation included animals that were out of the resting phase of their circadian rhythms. Minimal conductance of G. pusillus in the resting phase deviated by 14% less than the allometric expected value. This lower than predicted rate of conductance is in keeping with cricetids in general (Bradley and Deavers, 1980) and is also similar to measured rates of conductance in heteromyids (see Table 1; McNab, 1980).

Homeothermic maintenance

McNab (1970) suggests that in the evolution of small body size, an endotherm has two 'options'. Firstly it can reduce the precision of homeothermy by maintaining the relative levels of metabolism and conductance as dictated by its habits and environment. Secondly it can maintain a constant TB by means of a compensatory increase in the relative rate of metabolism or a compensatory decrease in the relative conductance. The ratio F, the percentage expected metabolism over the percentage expected conductance, may be used as an index of the maintenance of the relative degree of homeothermy (McNab, 1980). A ratio of 1 or above is indicative of a well developed and maintained endothermy. The F ratio of _G. pusillus_ (0.65) was similar to that of pocket mice, _Perognathus longimembris_ (Chew _et al._, 1967, Table 1). _Gerbillus pusillus_, like this pocket mouse, does not precisely maintain homeothermy. As expected, resting TB are lower than those measured when active; however when conditions are stressful, this gerbil becomes hypothermic and employs daily torpor (Buffenstein, in prep a & b). The observed low F ratio is, however, adequate when viewed in relation to the thermally stable climatic conditions _G. pusillus_ encounters in the tropics and in its burrow.

Summary

Thermoregulation was studied in *G. pusillus* at ambient temperatures ranging between 12 and 41 °C.

The thermal neutral zone for *G. pusillus* extended from 31.4 - 38.0 °C, with a basal oxygen consumption of 1.07 ± 0.03 cm^{3}O$_2$.g.$^{-1}$h.$^{-1}$.

Average TB remained constant (34.64 ± 0.12 °C) between 12 - 34 °C. However, above TA 34 °C, TB increased with increasing TA.

Evaporative water loss was stable below the TNZ (2.43 ± 0.07 cm^3 H O.g.$^{-1}$h^{-1}). Above 38.5 °C, evaporative water loss increased markedly and at 41 °C, it dissipated 63% of the metabolic heat produced.

Thermal conductance below thermoneutrality was constant (0.995 ± 0.21 J.cm.$^{-2}$h^{-1}). Between 30 °C and 39 °C, this coefficient of heat transfer from the animal to the environment was increased by behavioural and other means.

Gerbillus pusillus weighing approximately 13g, is equatorial, living in fairly warm burrows in a very sparsely vegetated area. Precision of homeothermy is not of the utmost importance as environmental temperatures do not vary drastically. This coupled with the fact that G. pusillus lives in an environment where food is often limiting, result in it having to conserve energy. Gerbillus pusillus therefore has a reduced BMR rate and a resting TB lower than most mammals.

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CHAPTER 3

The effect of starvation, food restriction and water deprivation on thermoregulation and average daily metabolic rates in *Gerbillus pusillus*.

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Running title: Torpor in *G. pusillus*

SUMMARY

1. Average daily metabolic rates (ADMRs) were monitored under several dietary conditions. *Gerbillus pusillus* demonstrated a 24-hour cycle of metabolic activity in phase with the photoperiod. When food and water were provided *ad lib.*, ADMR was 96.5% of the predicted value for a granivorous rodent. When deprived of water with an *ad lib.* supply of food, ADMR increased significantly. Unfavourable changes in these dietary regimes results in periodic bouts of hypothermia.

2. Gerbils on a restricted food intake maintained their weight after an initial loss of 7.93%. This negligible weight loss implies that *G. pusillus* uses hypothermia to regulate its metabolic rate to the energy available.

3. During periods of torpidity, metabolic rate was inversely related to temperature. The gerbils were unable to arouse below 15 °C. At this temperature co-ordination was poor. Metabolic rates of food restricted animals with body temperatures greater than 34.0°C did not differ from the minimal resting post absorptive rates under *ad lib.* food and water.

4 Arousal is not accompanied by an overshoot in oxygen consumption, implying that the overall rate of heat production is sufficient to warm the body tissue and accommodate the increased heat loss to the environment whilst body temperature returns to the coenothermic level.

5 At the natural burrow temperatures (30.0°C) torpid _G. pusillus_ would use 50% of the energy used in a coenothermic resting gerbil at the same temperature. Employment of torpor in its natural milieu would therefore confer a considerable saving in both energy and water loss.

INTRODUCTION

Gerbillus pusillus lives in a xeric environment where the mean annual temperature is above 27°C and is relatively stable throughout the year, as is indicated by the mean annual amplitude of 2-6°C (Gourou, 1970). Whilst temperature fluctuations are slight, food and water may be seasonally or irregularly scarce. Because of their small size, these animals cannot then migrate to more suitable environments and are therefore in an energetically precarious position. Any small mammal encountering unfavourable fluctuations in food and water supply should be under strong selection pressure to utilize hypothermia to reduce the high cost of living to within the levels of food availability. Indeed, many mammals are found to do this (Bartholomew, 1972; Tracy, 1977) although the physiological responses are quite variable (Hudson, 1978).

Dubois (1896) first started modern biological research on hypothermia in mammals, with his study on hibernation in marmots. Howard (1951) in a study on Peromyscus sp., first mentions shallow torpor resulting from lack of food and from low temperatures. In the first experimental study of torpidation, Petter (1955) found that when Gerbillus gerbillus from northern Africa became lethargic in the hot season, rectal temperatures were significantly depressed. Bartholomew and Cade (1957) confirmed these findings on Perognathus longimembris and suggested that, since lack of food appeared to be a cue for entrance into torpor, the observed hypothermia was simply a breakdown in thermoregulation due to an insufficient energy intake.

Subsequently much work has been done on the inducement of torpor, primarily on North American pocket mice and white-footed mice (Chew et al., 1965; MacMillen, 1965; Tucker, 1966; Morhardt and Hudson, 1966; Brower and Cade, 1971; Yousef and Dill, 1971a; Breyen et al., 1973; French, 1977; to name but a few). Virtually nothing is known about torpor in small rodents inhabiting the dry regions outside America (Lyman, 1978).

Despite the wealth of information on circadian rhythm in torpor (Chew et al., 1965; Morhardt and Hudson, 1966; Yousef and Dill, 1971b; Hill, 1975; Hudson, 1978; Hudson and Scott, 1979) little evidence has emerged to determine the prime function of torpor in desert mammals or even to determine if it is commonly employed in this environment. This paper attempts to answer this question by examining average daily metabolic rates (ADMRs) in G. pusillus under the different conditions, possibly encountered by this gerbil in its natural milieu. These include conditions of ad lib.

food and water; various combinations of food and/or water deprivation and finally the effect of a reduced food supply when water is freely available and when it is absent. This paper therefore presents one of the most comprehensive studies of the response of a single species to all the possible dietary conditions to which it may be exposed.

METHODS AND MATERIALS

AVERAGE DAILY METABOLIC RATES

Fifteen _G._ _pusillus_ were maintained in glass terraria containing river sand, nesting material and activity wheels in an air conditioned laboratory (24 ± 2 °C), with an approximate 24-hour photoperiod. Golden millet was supplied _ad_ _lib_. Free water was not provided and when the animals were not on a water restricted diet, fresh green vegetables and apples were supplied _ad_ _lib_.

Daily metabolic rates and torpor were studied under a variety of experimental conditions in 15 gerbils. Oxygen consumption was monitored by placing an animal in a clear perspex respiratory chamber (75mm by 160mm). This had a wire mesh platform on which the animal rested. The respiratory chamber was placed in a larger temperature (±1°C) and humidity (±2.0%) controlled chamber together with a similar respiratory chamber without an animal (the control). The temperature was maintained at 24°C and at a relative humidity of approximately 50% (the temperature and humidity of the laboratory in which the animals were maintained and therefore acclimated to). Each respiratory chamber was equipped with ports for a thermocouple and air vents. Air flowed through the respiratory chamber at $150cm^3$. min^{-1} and passed over a relative humidity probe (Vaisala humicap HM1-14). It was then dried over silica gel before being fed into an oxygen analyser, N-37 oxygen sensor, applied electrochemistry inc). The oxygen sensor monitored the difference in oxygen content between the respiratory chambers. The oxygen analyser, humidity probe and thermocouples were connected to a data logger (Esterline Angus P.D.2064) which recorded these measurements every 15 minutes over a 24-hour period. The chamber was equipped with a viewing port enabling behavioural observations and the measurement of the respiratory rate.

All 15 gerbils were subjected to the same experimental treatments. However ADMRs of eight from this "pool" were monitored under the following experimental conditions:-

ADDENDUM★

Average daily metabolic rate (as originally defined by Pearson, 1947) includes basal metabolism, thermoregulatory metabolism, specific dynamic action and activity metabolism. This was calculated to be the average of the twenty-four mean hourly readings of oxygen consumption (Gessaman, 1973; Grodzinski and Wunder, 1975).

Pearson, O.P. 1947. The rate of metabolism of some small mammals.
Ecology 28 : 127-145.

(A) *Ad lib*. food and water:

Gerbillus pusillus previously maintained in the laboratory on an *ad lib*. food and water diet were placed in the metabolic chamber and left to habituate for an hour, during which time *ad lib*. food and water was supplied. The water source (lettuce) was removed at the beginning of the experiment and resupplied, for 30 minutes, at the beginning and end of the dark phase of the 24-hour cycle. Removal of lettuce enabled valid humidity measurements to be taken during the rest of the 24-hour experimental period.

(B) No food but *ad lib*. water:

The same experimental procedure as described in (A) but with both food and water removed at the onset of the experiment and only water supplied at the beginning and end of the dark phase.

(C) *Gerbillus pusillus* deprived of water with *ad lib*. food:

Gerbils were maintained in the laboratory for at least 14 days without exogenous water before ADMR was measured.*

(D) Gerbils deprived of water with no food or water during the measurement of ADMR:

The same procedure as in (C), the gerbils were deprived of water for at least 14 days prior to experimentation.

No food or water was supplied during the 24-hour experimental run.

(E) Food restricted to one third of the normal ration plus _ad lib_. water:

Gerbillus pusillus were maintained on this restricted diet for at least 48 hours prior to being placed in the metabolic chamber. Exogenous water was supplied as described in (A).

(F) Gerbils deprived of water on a diet restricted to one third the normal ration:

This involved the same food procedure as in (E) and the water deprivation procedure was the same as in (C).

During all of the above experiments rectal temperatures were only taken intermittently because handling disturbed the torpid mice and usually induced arousal.

The ADMRs were first monitored when water was freely available. Once these were complete, the gerbils were gradually deprived of water over an eight day period. Thereafter no free water was supplied. The monitoring of ADMR only recommenced once daily weight loss was negligible (14 days after all free water was withheld).

DETECTION OF TORPOR

Nest temperatures of four gerbils on both ad lib. and food restricted (0.5g.day^{-1}) diets were monitored by placing thermocouples in their nests. Temperatures were taken every 15 minutes and temperature changes due to the animal leaving the nest could be differentiated from the more gradual torpor-related changes in nest temperature.

TORPOR

The effect of ambient temperature on body temperature and oxygen consumption during torpor was determined in G. pusillus exhibiting regular daily bouts of torpor. These were examined during the day. Torpid animals were exposed to four different ambient temperatures (15, 20, 24 and 34°C). At each new ambient temperature, a gerbil was left in the respiratory chamber for one hour prior to monitoring the rate of oxygen consumption. Thereafter, oxygen consumption was monitored at five minute intervals for at least three hours. The lowest ten readings for each animal at each ambient temperature, corrected to STP, was assumed to be the rate of oxygen consumption during hypothermia. Rectal temperatures were taken immediately on terminating the run.

Statistical analyses included analysis of variance, student t-tests and paired t-tests where applicable (Zar, 1974). Data were considered statistically significant at a probability level of 5%. Unless otherwise stated mean values and standard errors are given.

RESULTS

TORPOR

Reduced body temperature was first observed in *G. pusillus* under non-experimental conditions. This was most pronounced in gerbils that had escaped from their cages during the night and were found the next morning on the cold cement floor. Despite the fact that most of the escapees had an *ad lib*. supply of food and water in their cages, these animals were sluggish and easy to catch. Rectal temperatures were all below the coenothermic levels. On returning to their cages shivering was observed, whilst the gerbils ate continuously. In all six recorded cases body temperature had risen in 20 minutes from 24-26°C to within 1°C of the observed average TB (34.6°C). Other instances of torpor occurred under experimental conditions of dietary stress. These initial observations of torpor prompted further study.

NEST TEMPERATURE

Nest temperatures measured during torpor, gradually decreased after 4am and then levelled out at a temperature 4°C lower than that of the same gerbil on *ad lib*. food (Fig. 1).

AVERAGE DAILY METABOLIC RATES

No significant differences were found in the variation of ADMR between male and female *G. pusillus* ($p \geq 0.10$). Data was consequently pooled.

THE ADMRS FOR EUTHERMIC GERBILS.

Analysis of variance confirmed the significantly different responses to the first four experimental treatments where gerbils were maintained on an *ad lib*. seed diet (Table 1, Fig. 2, 3, 4, & 5). The three stressful conditions, namely, water deprivation plus *ad lib*. food (B), *ad lib.* water but no food (C), and no food and no water (D), were not significantly different

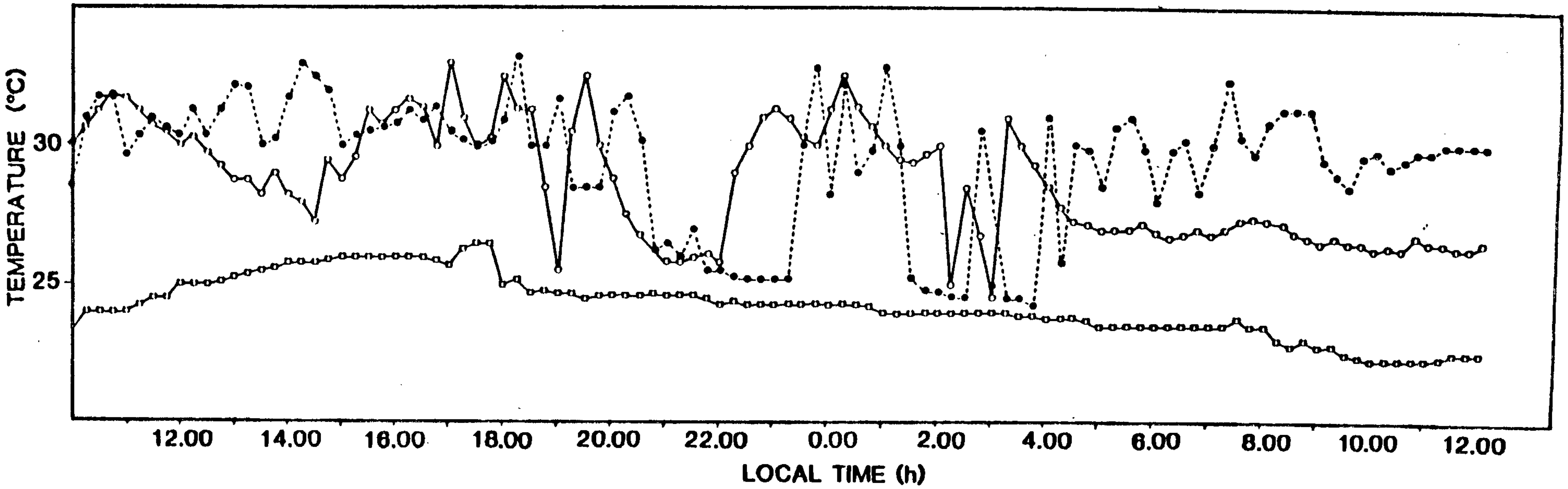


Figure 1 : Ambient temperature (□) and nest temperatures monitored in the same gerbil when euthermic (●) and when hypothermic (o)

Figure 2 : Representative records of oxygen consumption in eight *Gerbillus pusillus* when food and water are supplied *ad lib.* (A). The scotophase was set at between 19h00 and 07h00. The average daily metabolic rate for each individual is given in the upper right hand corner of each block.

Figure 3 : Representative records of oxygen consumption in eight *Gerbillus pusillus* when provided with *ad lib.* food but deprived of water for 14 days (B). The scotophase was set at between 19h00 and 07h00. The average daily metabolic rate for each individual is given in the upper right hand corner of each block.

TABLE 1 Effect of diet on average daily metabolic rate (ADMR) during euthermia and hypothermia. All values are expressed in cm^3 oxygen g^{-1} h^{-1}.

Experimental condition	Number of animals excluded	ADMR ($ml\ O_2.g^{-1}.h^{-1}$)		Minimum value ($ml\ O_2.g^{-1}.h^{-1}$)		Maximum value ($ml\ O_2.g^{-1}.h^{-1}$)		Animals excluded
		$\bar{x}$	$\pm$ SE	$\bar{x}$	$\pm$ SE	$\bar{x}$	$\pm$ SE	
Euthermic gerbils								
A. + FOOD/ + WATER	8	4.06	0.08	3.20	0.06	5.04	0.12	0%
B. + FOOD/ - WATER	6	5.47	0.23	3.64	0.23	7.20	0.37	25%
C. - FOOD/ + WATER	5	4.35	0.19	3.08	0.17	5.86	0.43	38%
D. - FOOD/ - WATER	1	4.76	-	3.08	-	5.64	-	88%
E. $\frac{1}{3}$ FOOD/ + WATER	0	-	-	-	-	-	-	100%
F. $\frac{1}{3}$ FOOD/ - WATER	0	-	-	-	-	-	-	100%
Torpid gerbils								
A. + FOOD/ + WATER	0	-	-	-	-	-	-	100%
B. + FOOD/ - WATER	2	3.34	0.22	1.94	0.01	4.31	0.19	75%
C. - FOOD/ + WATER	3	3.86	0.19	1.18	0.41	5.89	0.34	62%
D. - FOOD/ - WATER	7	3.80	0.27	0.94	0.21	5.72	0.26	12%
E. $\frac{1}{3}$ FOOD/ + WATER	6	1.83	0.19	0.41	0.05	4.91	0.24	0%
F. $\frac{1}{3}$ FOOD/ - WATER	6	1.73	0.23	0.38	0.06	5.12	0.34	0%

Figure 4 : Representative records of oxygen consumption in eight non water-stressed *Gerbillus pusillus* when food is withheld during the 24-hour period of monitoring (C). The scotophase was set at between 18h00 and 07h00. The average daily metabolic rate for each individual is given in the upper right hand corner of each block.

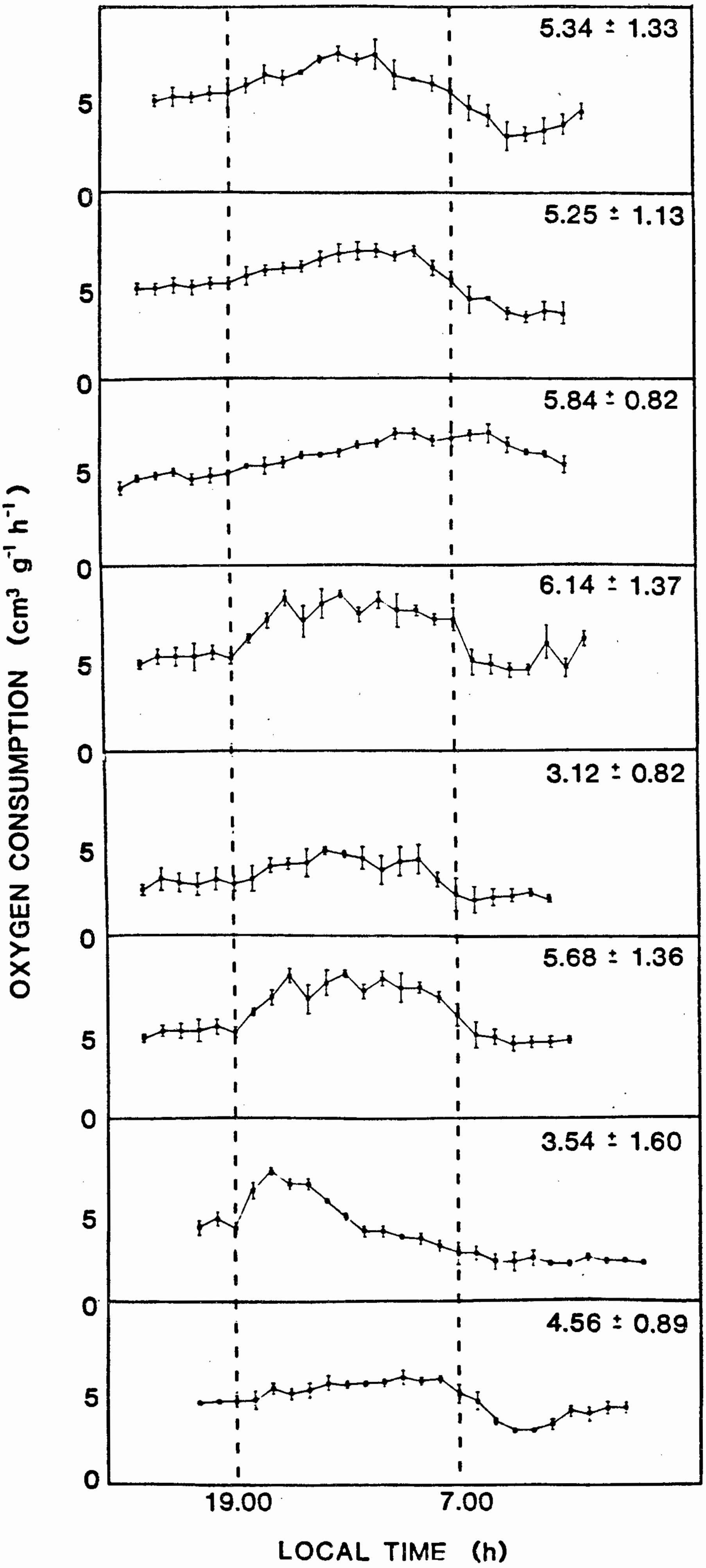

5.34 ± 1.33
5.25 ± 1.13
5.84 ± 0.82
6.14 ± 1.37
3.12 ± 0.82
5.68 ± 1.36
3.54 ± 1.60
4.56 ± 0.89
5
0
OXYGEN CONSUMPTION (cm³ g⁻¹ h⁻¹)
19.00
7.00
LOCAL TIME (h)

Figure 5 : Representative records of oxygen consumption in eight *Gerbillus pusillus* that have been deprived of water for 14 days when food is withheld during the 24-hour period of monitoring (D). The scotophase was set at between 19h00 and 07h00. The average daily metabolic rate for each individual is given in the upper right hand corner of each block.

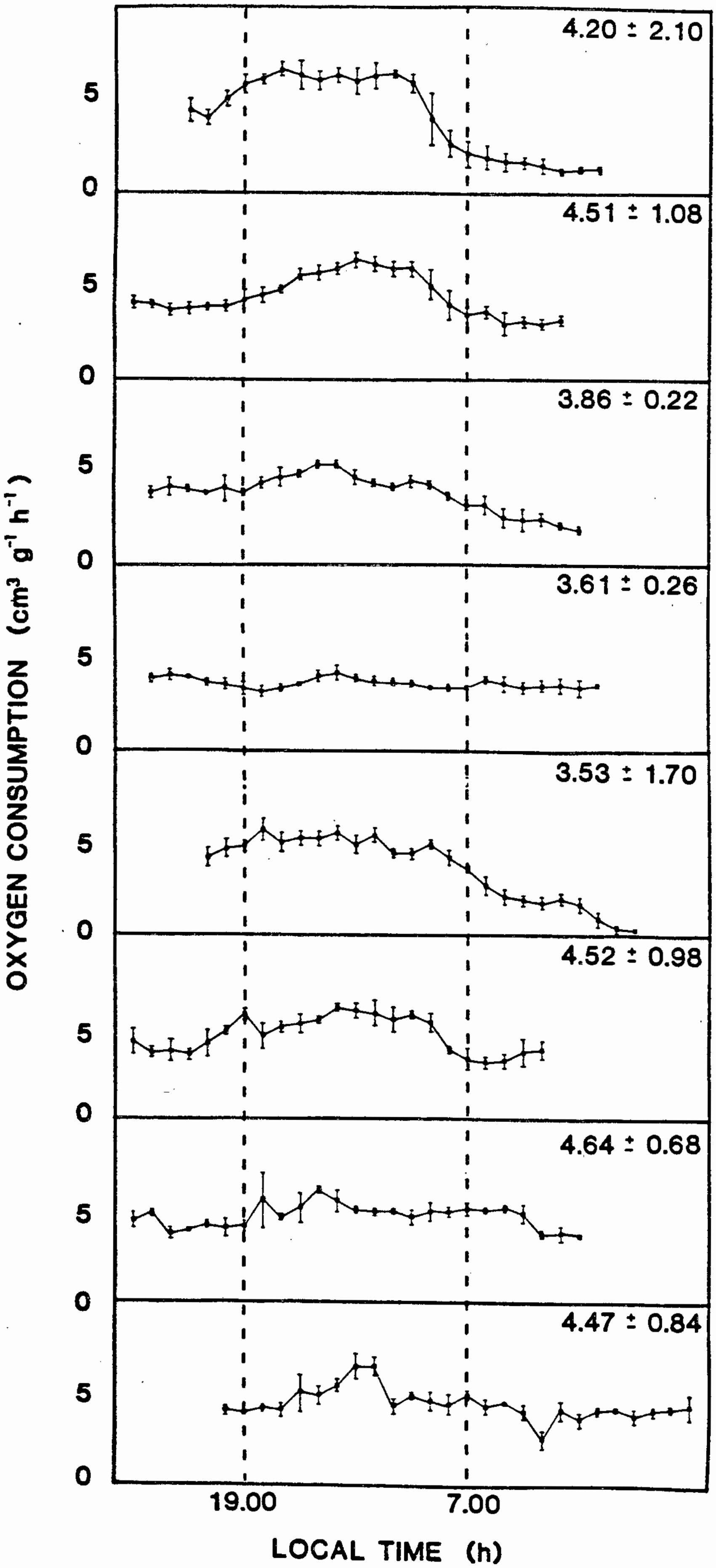
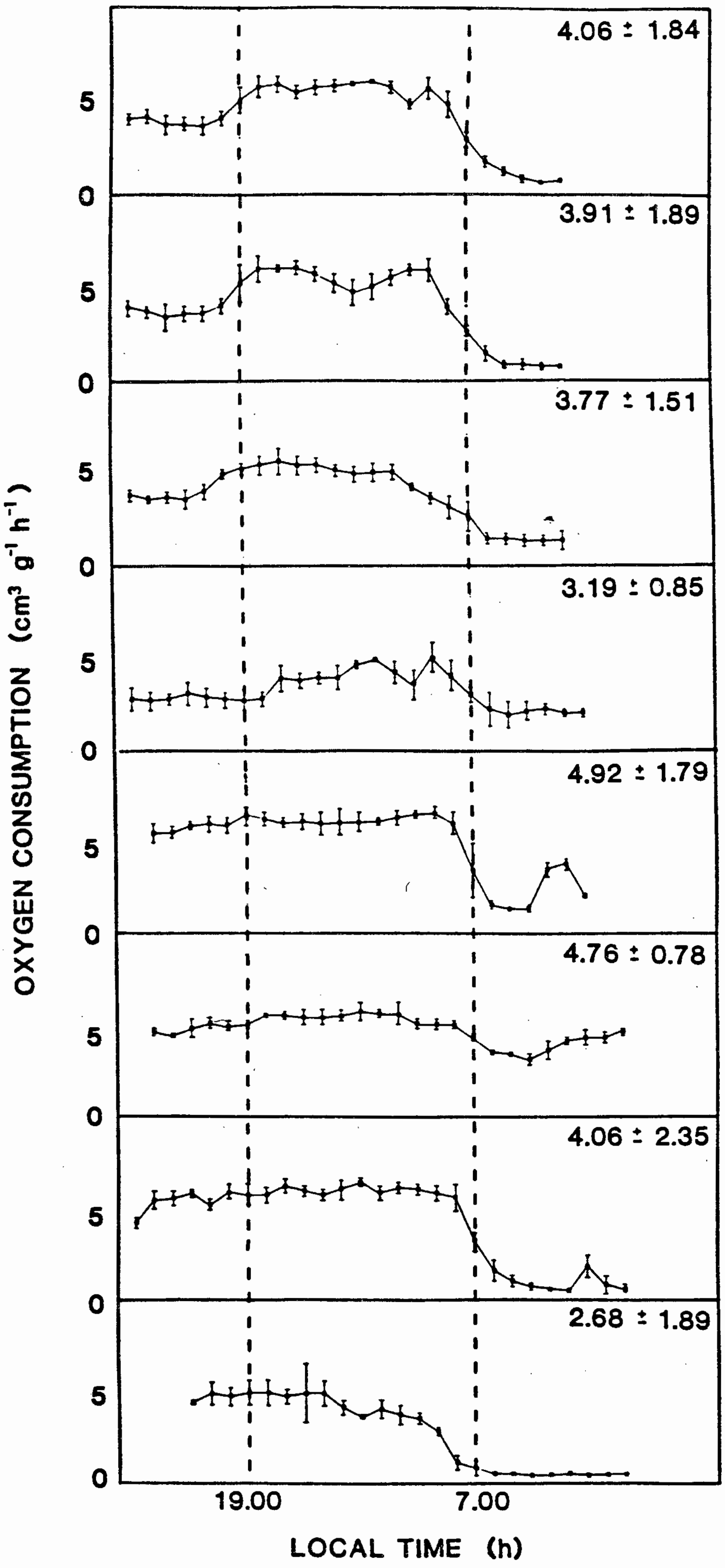

4.20 ± 2.10
4.51 ± 1.08
3.86 ± 0.22
3.61 ± 0.26
3.53 ± 1.70
4.52 ± 0.98
4.64 ± 0.68
4.47 ± 0.84
5
0
OXYGEN CONSUMPTION (cm³ g⁻¹ h⁻¹)
19.00
7.00
LOCAL TIME (h)

Figure 6 : Representative records of oxygen consumption in six *Gerbillus pusillus* when water is freely available but food is restricted to 0.5 g millet per day (E). The scotophase was set at between 19h00 and 07h00. The average daily metabolic rate for each individual is given in the upper right hand corner of each block.


4.06 ± 1.84
3.91 ± 1.89
3.77 ± 1.51
3.19 ± 0.85
4.92 ± 1.79
4.76 ± 0.78
4.06 ± 2.35
2.68 ± 1.89
5
0
OXYGEN CONSUMPTION (cm³ g⁻¹ h⁻¹)
19.00
7.00
LOCAL TIME (h)

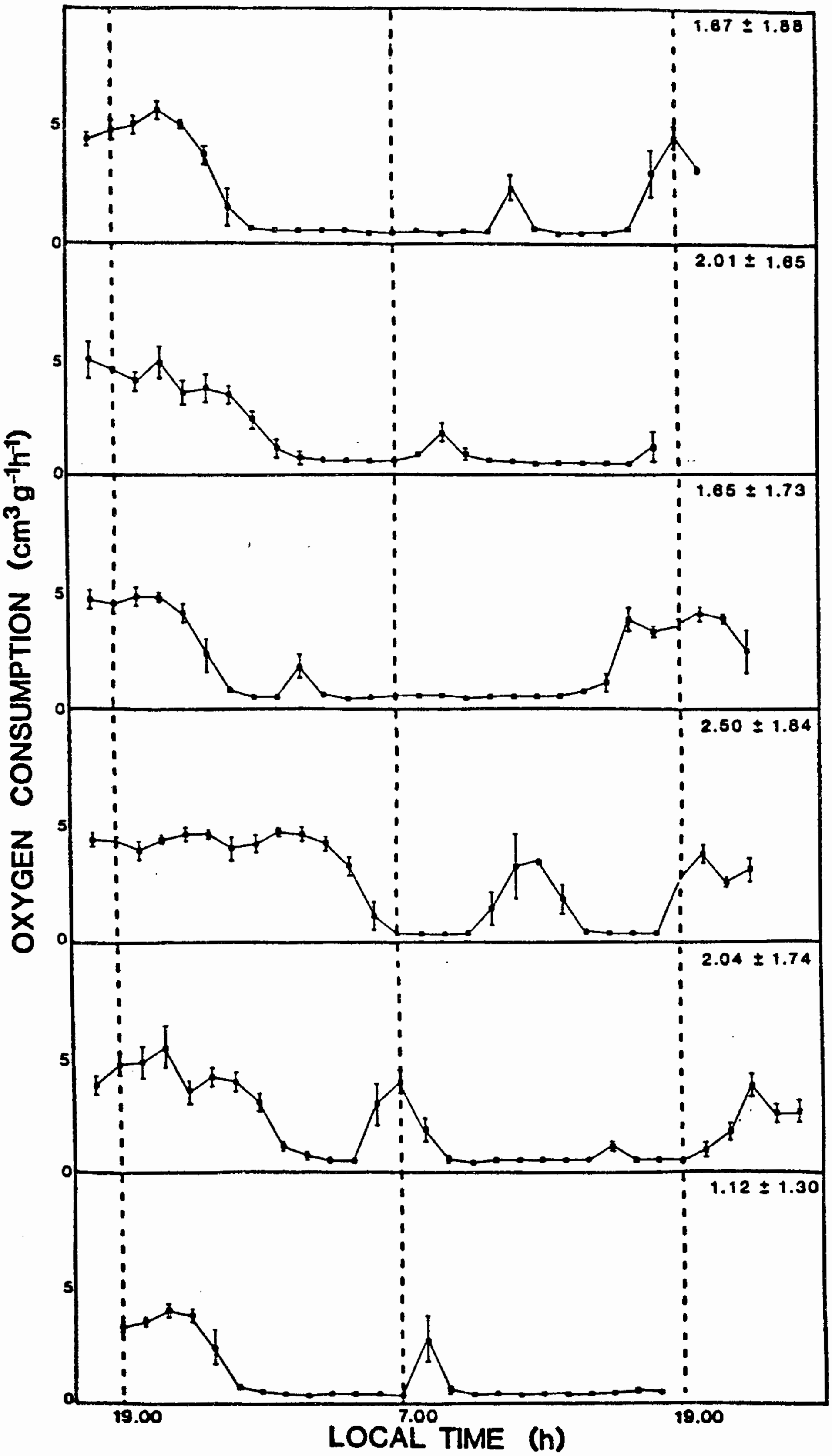
from each other ($p \geq 0.05$). When the gerbils were maintained on an ad lib. supply of millet and water but were starved during the 24-hour period of monitoring (C), the ADMR values obtained were not significantly different to those measured under any of the treatments where animals were maintained on a diet with ad lib. food.

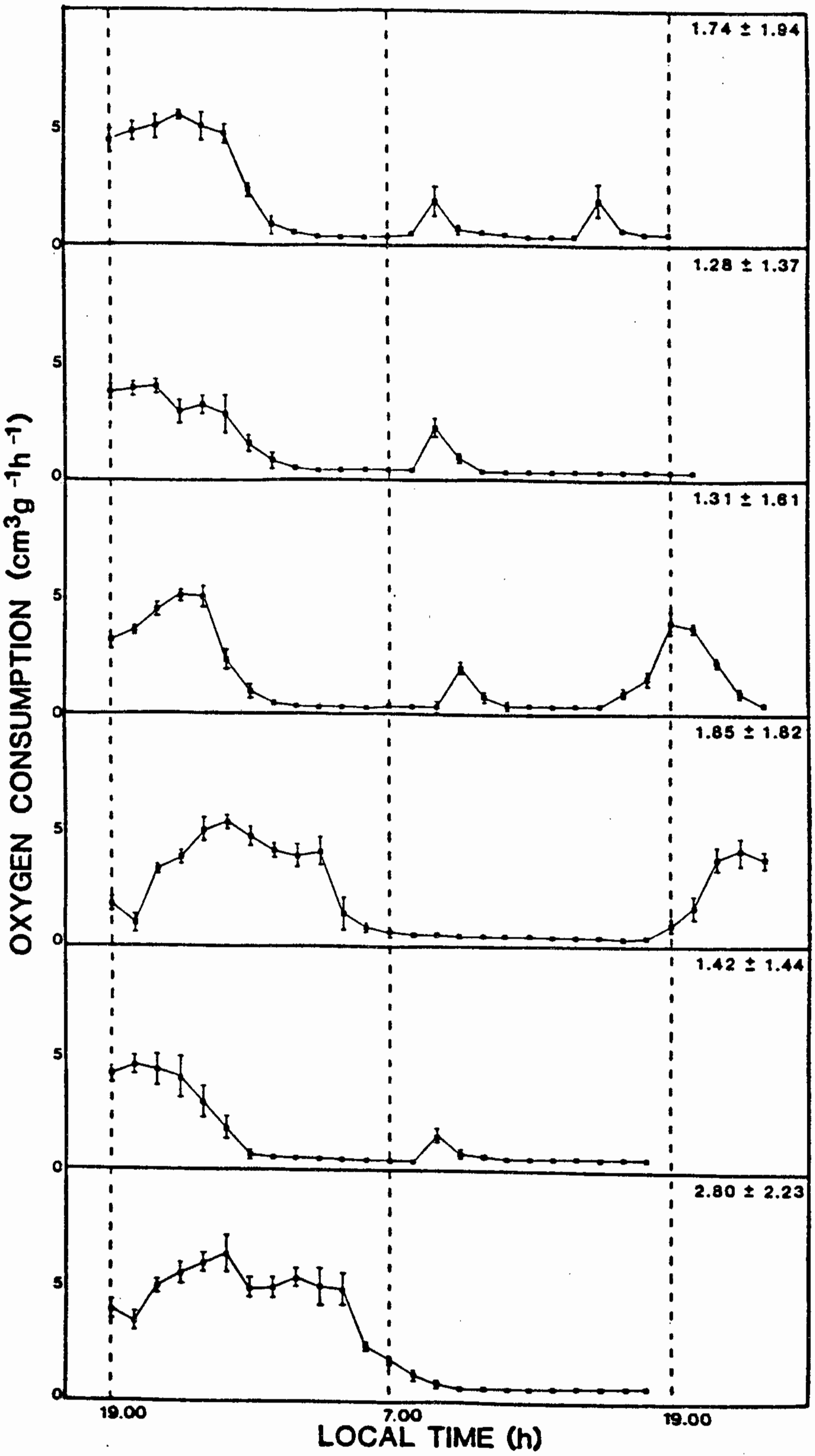
The ADMRs monitored in rodents deprived of water were similar, irrespective of whether food was supplied or withheld during the period of monitoring. These were however, significantly different to those measured when food and water were freely supplied ($P \leq 0.01$).

ADMRS FOR HYPOTHERMIC GERBILS.

No gerbils supplied with ad lib. food and water became hypothermic (Table 1, Fig. 2). When deprived of water with no food provided during the experimental run (D) 83.33% of the gerbils became torpid (Fig. 5), 33% employed torpor in response to treatment B (ad lib. water but no food supplied during the period monitored) and 20% became torpid (Fig. 4) when rodents were deprived of water but supplied with ad lib. food (C). The ADMRs of these torpid animals were not significantly different from each other.

Figure 7 : Representative records of oxygen consumption in six *Gerbillus pusillus* when deprived of water for at least 14 days and maintained on a restricted dietary intake of 0.5 g per day (F). The scotophase was set at between 19h00 and 07h00. The average daily metabolic rate for each individual is given in the upper right hand corner of each block.


1.67 ± 1.88
2.01 ± 1.65
1.65 ± 1.73
2.50 ± 1.84
2.04 ± 1.74
1.12 ± 1.30
OXYGEN CONSUMPTION (cm^{3}g^{-1}h^{-1})
5
0
19.00
7.00
19.00
LOCAL TIME (h)


1.74 ± 1.94
1.28 ± 1.37
1.31 ± 1.61
1.85 ± 1.82
1.42 ± 1.44
2.80 ± 2.23
5
0
OXYGEN CONSUMPTION (cm³g⁻¹h⁻¹)
19.00
7.00
19.00
LOCAL TIME (h)

A restricted food supply of 0.5g of golden millet with an _ad lib._ supply of water (E), induced the onset of torpor within 48 hours in 88% of the gerbils under investigation. By the third day all _G. pusillus_ had become torpid for at least nine hours each day (Fig. 6 & 7). Similarly, all water deprived and food restricted gerbils (F) underwent torpor within two days.

The ADMRs of gerbils maintained on a restricted daily intake of 0.5g of millet, were similar irrespective of whether water was freely available or whether they were water deprived (E and F, Figs. 6 & 7). These ADMRs were significantly lower ($p \leq 0.01$) than those when the gerbils were maintained on an _ad lib._ seed supply (A,B,C,D), enabling considerable savings in energy expenditure (Table 2).

Evaporative water loss per ml oxygen consumption was not significantly different ($p \geq 0.05$) during either hypothermia or coenothermia (Table 2). In absolute terms, however, a considerable saving in water loss occurred and was a direct result of reduced oxygen consumption.

TABLE 2 Estimated savings in energy and evaporative water loss realised by torpor in the laboratory at 24°C

	Ad lib. food & water		Restricted food intake but *ad lib.* H_2O		Saving by use of torpor	Saving as a percentage total daily intake in the absence of torpor
	$\bar{x}$	$\pm$ S.E.	$\bar{x}$	$\pm$ S.E.		
Total daily oxygen consumption ($m\ell\ O_2.g^{-1}.day^{-1}$)	98.11	3.18	40.64	4.01	57.47	58.60
Evaporative water loss ($m\ell\ H_2O.m\ell O_2^{-1}$)	1.21	0.09	1.15	0.29	0.06	5.00
Daily evaporative water loss ($mg\ H_2O.day^{-1}$)	118.71	-	45.92	-	72.79	61.31

ENTRY INTO TORPOR

Entry into torpor occurred when activity was at a low level, usually in the dark hours of the early morning. It was gradual, taking as long as six hours to reach minimal oxygen consumption levels (Figs. 5 & 6).

AROUSAL FROM TORPOR

Duration and depth of torpor were extremely variable. In some instances the slightest disturbances triggered off arousal whereas at other times forced arousal was more difficult. The depth of torpor appeared to be dependent on the ambient temperature, body temperature and the time from entering into torpor. The lower the air and body temperature, the deeper the torpor. Rodents were easily aroused shortly after becoming hypothermic.

During arousal gerbils shivered continuously. This stopped at a body temperature greater than 31 °C. If food was available at ambient temperatures greater than 24 °C, the gerbils ate continuously. It can be seen from Figs. 6 and 7 that oxygen consumption increased approximately 12-fold from the torpid value to a maximum 2-3 hours after food was placed in the chamber and then dropped slightly. The increase in oxygen consumption was accompanied by a four-fold increase in respiratory frequency (from 42.55 ± 2.53 to 187.22 ± 7.49 (n=6) breaths per minute). This was 2.07 times the respiratory frequency of post absorptive resting gerbils. Body temperature rose by 0.65 ± 0.05 $^\circ C.min^{-1}$ (n=6), during the time of the most rapid increase in body temperature.

Oxygen consumption during arousal did not exceed the maximum levels used before entry into torpor. However, after peaking, the oxygen consumption dropped slightly and fluctuated about that elevated range (±3.6 $cm^3O_2.g^{-1}.h^{-1}$).

EFFECT OF TEMPERATURE ON TORPOR

Oxygen consumption in hypothermic gerbils was directly proportional to air and body temperature (Fig. 8 & 9). The equations relating these parameters are:

$$VO_2(cm^3O_2.g^{-1}.h^{-1}) = -0.38 + 0.037TA(^\circ C) \quad r=0.91 \quad n=30$$

$$VO_2(cm^3O_2.g^{-1}.h^{-1}) = -0.67 + 0.044TB(^\circ C) \quad r=0.94 \quad n=30$$

VO_2 is the rate of oxygen consumption ($cm^3.g^{-1}.h^{-1}$), TA is the ambient temperature (°C) and TB is body

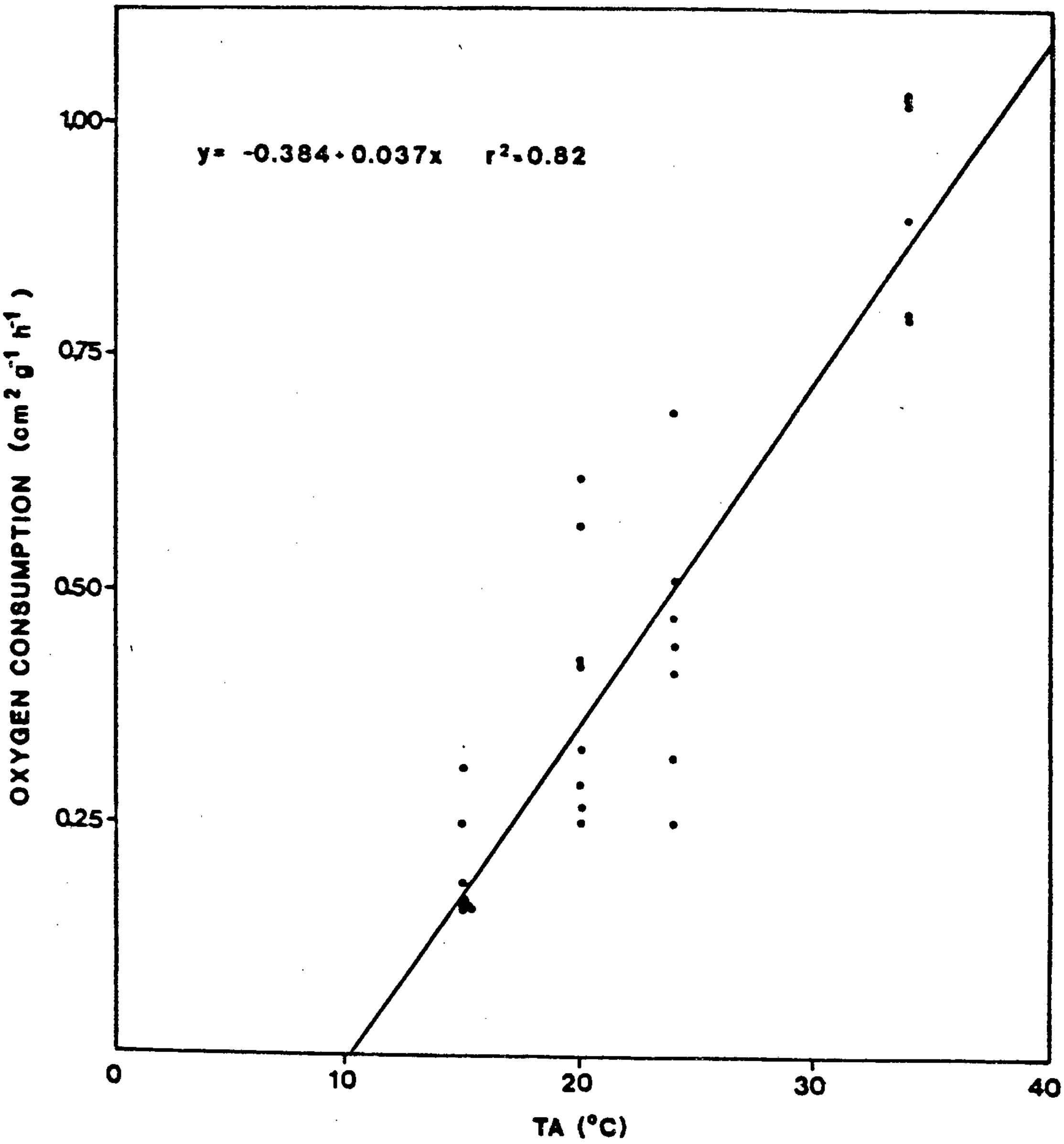


Figure 8 : The effect of ambient temperature (TA) on the rates of oxygen during torpor in *Gerbillus pusillus*.

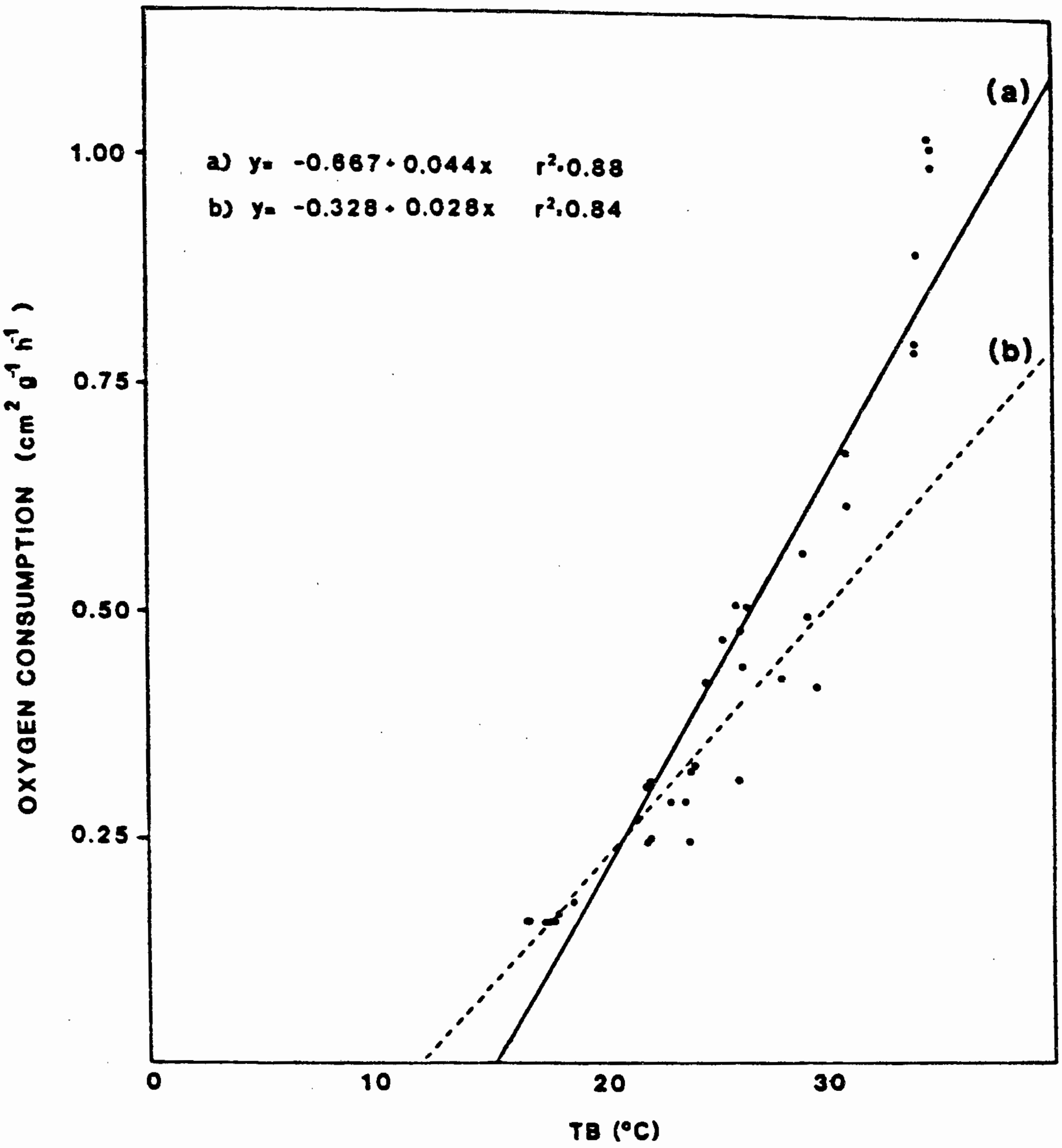


Figure 9 : The effect of body temperature (TB) on the rates of oxygen consumption during torpor in *Gerbillus pusillus*. Line (a) is the equation in which body temperatures within the cenothermic range are included and line (b) is the linear equation which has excluded body temperatures within the cenothermic range.

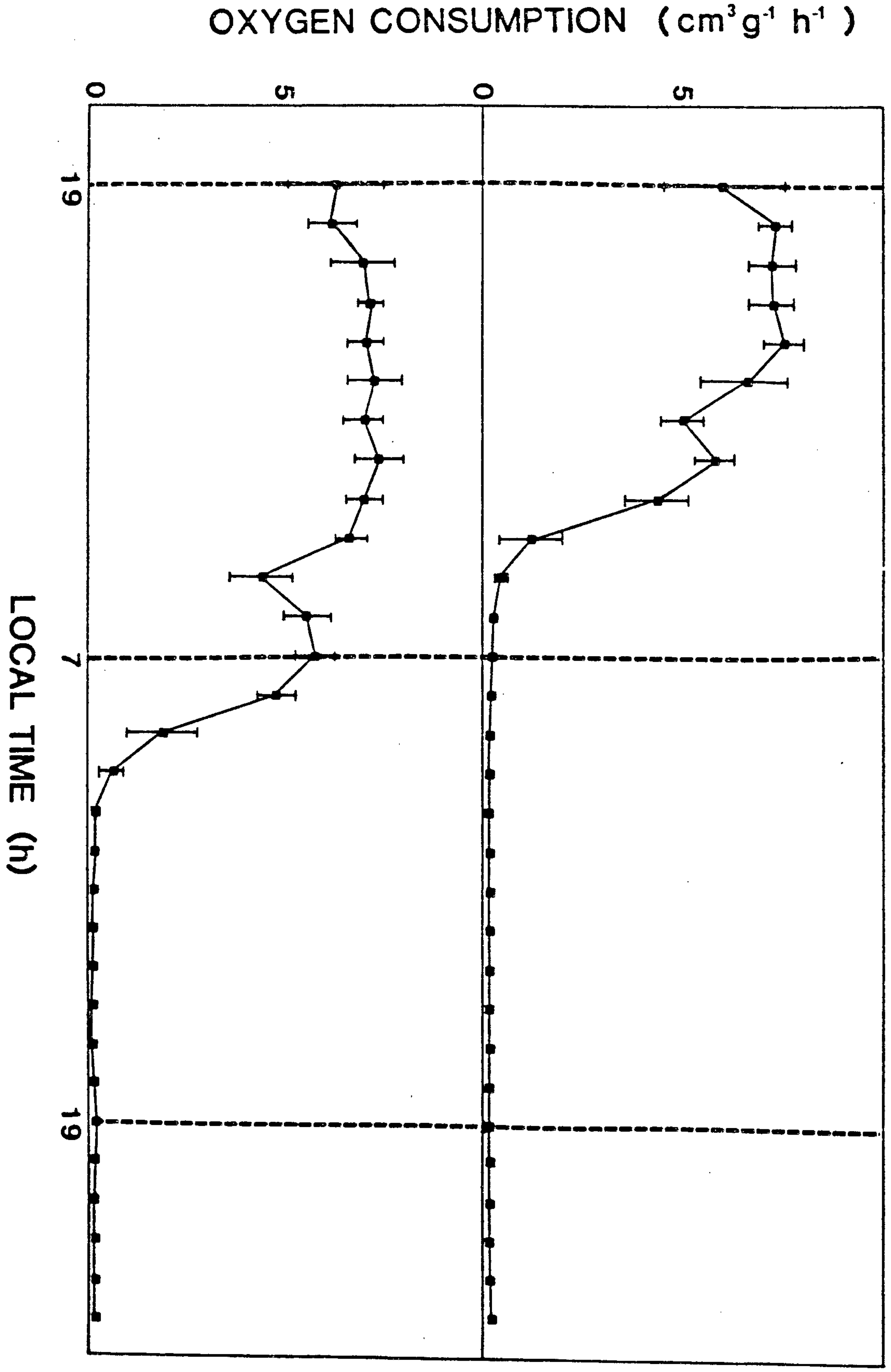
temperature (°C). The higher the body temperature, the more shallow the torpor. The Q_{10} (as determined from Fig. 8) for oxygen consumption in food restricted gerbils was 3.07.

Torpid gerbils resemble sleeping gerbils, in that they adopt the same spheripsoid posture. Torpor can however be distinguished from somnolescence in that breathing is slower and irregular. Similar arhythmia has been reported (Bartholomew and Cade, 1957). Within the thermoneutral zone, oxygen consumption of torpid animals was similar to data from post-absorptive resting gerbils ($p \geq 0.05$). Torpor could therefore not be distinguished from somnolescence. If oxygen consumption readings for animals with body temperatures above 30°C are therefore excluded, the Q_{10} for torpid gerbils is 2.2. The equation for this is:-

$$VO_2 (cm^3 O_2 . g^{-1} . h^{-1}) = -0.33 + 0.028TB(°C) \quad r=0.92 \quad n=22$$

VO_2 is the rate of oxygen consumption and TB is body temperature.

The lowest body temperature recorded was 16.7. At this temperature, animals were lethargic and uncoordinated, being unable to right themselves if placed on their sides. They remained torpid for 20 hours (Fig. 10) and then were removed from the experimental chamber


OXYGEN CONSUMPTION (cm³g⁻¹ h⁻¹)
0
5
0
5
19
7
19
LOCAL TIME (h)

(ambient temperature = 15°C), and returned to room temperature (23.5°C) where they aroused themselves to a coenothermic state within forty minutes.

DISCUSSION

ADMR

Physiologically ADMR is not a well defined parameter; it is, however, an operationally useful artificial measurement of metabolism under laboratory conditions (Grodzinski and Wunder, 1975). Measurements of ADMRs necessitate at least 24 hours of monitoring oxygen consumption and so include energy expenditure from resting basal metabolism, voluntary activity and digestion of available food (Gessaman, 1973).

Gerbillus pusillus has a 24-hour cycle of oxygen consumption in phase with the photoperiod (Figs. 2, 3, 4 & 5) with the lowest levels occurring during the light phase. With *ad lib*. food and water available to the gerbil, minimal oxygen consumption did not fall below the minimal resting metabolic rate ($2.63 cm^3 O_2 . g^{-1}.h^{-1}$) extrapolated from the equation taken from

Buffenstein and Jarvis (in press)

$$VO_2(cm^3O_2.g^{-1}.h^{-1}) = 7.753 - 0.2134\ TA(°C)$$

VO is the rate of oxygen consumption and TA is ambient temperature. Mean ADMR was 4.06 + 0.7 (n=8) $cm^3O_2.g^{-1}.h^{-1}$ at 24°C. This is 96.5% of the expected value (Grodzinski and Wunder, 1975) calculated from a temperature corrected equation for granivorous rodents (Table 3).

EFFECT OF HYDROPENIA ON ADMR IN NON-TORPID GERBILS.

Despite the fact that *G. pusillus* had been maintained in the laboratory for three months without any exogenous source of water and could therefore be considered to be independent of the exogenous water supply, non-torpid, water stressed animals had significantly higher ADMRs ($p \leq 0.002$) than under *ad lib.* conditions. Similar rates have been observed in other rodents (Grimsley, 1965; Bintz and Roesbury, 1978).

The increased ADMR recorded from gerbils under stressful conditions at first appears to be an anomaly. However, this is due to an initial rise in searching activity for water and food. If this proves unsuccessful *G. pusillus* will then resort to

TABLE 3 Average daily metabolic rates (ADMR) in several rodents at 20°C when provided with *ad lib.* food and water

Species	Mass g	ADMR $cm^3 O_2.g^{-1}.h^{-1}$	% Expected #	Source
Perognathus longimembris	8.2	6.87	99	Chew *et al.*, 1965
Micromys minutus	8.7	5.75	85	Gorecki, 1971
Reithrodontomys megalotis	9.0	6.32*	95	Chew & Chew, 1970
Gerbillus pusillus	12.6	5.38*	96	Present study
Pitymus subteraneus	13.0	5.61	101	Gebczyński, 1964
Mus musculus	17.0	5.30*	110	Morrison & Ryser, 1951
Perognathus formosus	18.0	4.00	85	Chew *et al.*, 1965
Peromyscus maniculatus gracilis	19.0	4.20	92	Morrison & Ryser, 1951
Clethrionomys gapperi	21.0	4.70*	108	Morrison & Ryser, 1951
Clethrionomys rutilus	25.0	3.61*	91	Grodzinski, 1971
Apodemus flavicollis	32.0	3.37	96	Gebczyński, 1966

Calculated from Grodzinski and Wunder (1975) allometric equation :

$$\text{ADMR } (cm^3 O_2.g^{-1}.h^{-1}) = 19.94\ W_{(g)}^{-0.50}$$

* Corrected for temperature adjustment to 20°C as in Morrison and Ryser (1951)

hypometabolism. This is suggested by the fact that under experimental condition, D, the most harsh experimental milieu 83.3% animals had to be excluded from the data because they became torpid.

TORPOR

Decrease in thermoregulatory control under water or food restriction is a common occurrence (Hudson, 1967; Kenagy, 1973; Walton and Andrews, 1981) and is thought to result primarily from inadequate energy intake (Brown and Bartholomew, 1969; Mullen, 1971) and this was the norm for _G. pusillus_. However, there were exceptions and two _G. pusillus_ deprived of water with _ad lib._ food, became hypothermic whilst in the respiratory chamber. Similar voluntary hypothermia in the presence of _ad lib_. food has also been reported by Tucker (1962), MacMillen (1972), Hill (1975), Vogt and Lynch (1978). Heldmaier and Steinlechner (1981) stress individual variation within a population, and suggest that the employment of torpor in some individuals guarantees survival of a sufficient fraction of the population during unfavourable periods.

Small size presents several energetic problems for homeotherms in that metabolic rate and energy of activity are inversely proportional to mass. Exchange of heat outside the thermoneutral zone is high because small size limits the amount of insulatory pelage on the animals. Consequently, the maintenance of a constant body temperature is energetically high, requiring a greater minimum daily food intake per unit size.

There is considerable variation in the degree to which _G. pusillus_ permits its body temperature to drop. Such variation in body temperature is common in torpid rodents (Wang and Hudson, 1970; Lynch _et al._, 1978a and b). The drop in body temperature is also dependent to a large extent on the duration of exposure to starvation or the inadequate food supply.

When on a restricted food intake _G. pusillus_ lost 7.93 + 0.55% of its body weight during the first two days. Thereafter, weight loss became negligible in the torpid animals. _Gerbillus pusillus_ remained torpid for 77% of the day (Table 1), by doing so, it was able to maintain its mass. Arousal from torpor is metabolically expensive. However, in small rodents, it represents only a small fraction of the average daily oxygen consumption compared to the energy requirements of a larger species such as a ground squirrel (Bartholomew, 1982). Employment of torpor for _G. pusillus_ enabled a saving of approximately 58.6% of the oxygen consumption under _ad lib._ food and water conditions. This saving will increase as the length of bouts of torpor increases in response to dietary inadequacies (Tucker, 1966; Kenagy, 1973; Hudson, 1978). This adjustment to nutritional supply may account for the considerable variability observed.

Unfortunately, no work has been done on the energy utilization of torpid animals under natural conditions. Because the kinds and intensities of selection pressures acting on a species vary, it is to be expected that both body temperature and the duration of torpor will be modified to adapt a particular species to the availability of food in its niche. Acclimation to drought and seasonal fluctuations is a common occurrence with several species actually anticipating times of unfavourable food supply (Bartholomew, 1972).

Gerbillus pusillus entered torpor in the early hours of the morning and emerged from bouts shortly after dark. This regime potentially enables the use of the entire dark period for foraging. If energy requirements are not met during foraging, torpor may be resorted to again, so making food reserves last longer.

The correlation between dry seasons and the use of aestivation in desert rodents has been used as infacto evidence that a lack of moisture may induce torpidity (Hudson and Bartholomew, 1964). This seems incongruous, however, as *G. pusillus* and many other known aestivators have been found to survive indefinitely (more than 12 weeks in the case of *G. pusillus*) on a diet of dry seed. *Gerbillus pusillus* has an efficient urine concentrating ability (Buffenstein in press) and this coupled with a depressed metabolic rate and the resulting decrease in evaporative water loss should enable it to maintain a positive water balance. In most cases where torpor is attributed to the scarcity of water, there is a concomitant decrease in food supply. Lynch *et al*. (1978a and b) and Hudson (1973) suggests that drought triggers spontaneous torpor primarily because of the threat of an inadequate food supply. In *G. pusillus* and most probably other torpid small mammals, a reduction in metabolic rate whilst using available energy parsimoniously is also accompanied by a considerable saving in water. An aestivating animal is in a thermodynamically steady state with its environment when body temperature approximates ambient. This is the most energetically efficient state conferring a considerable saving by reducing the production of metabolic heat. It also results in a decrease in metabolic water production and, because fewer breaths are taken, pulmocutaneous water loss is concomitantly reduced. Furthermore, as body temperature approaches ambient temperature, the temperature difference between inhaled and expired air is minimal, as is the relative humidity, so diminishing evaporative water loss still further.

However, it should be realised that these savings are absolute rather than relative. For in both torpid and non-torpid G. pusillus at ambient temperature 24°C, evaporative water loss per ml oxygen consumed was similar. The overall savings in water were only significant because oxygen consumption was depressed.

Gerbillus pusillus is predominantly a granivorous rodent. In its natural environment seed production is limited to certain times of the year and sometimes may not occur for several consecutive years. Consequently, these gerbils must be able to carry out all essential functions on a limited energy supply. This situation renders strict maintenance of homeothermy self-defeating. Instead voluntary hypothermia is used. When food is in abundance, G. pusillus do not become torpid, but when this supply is limiting, it resorts to varying bouts of torpor whose length is dependent on available energy. Gerbillus pusillus conforms to the generalized characteristics of aestivators (Hudson and Bartholomew, 1964). High lower critical temperatures and reduced minimal metabolic rates in the thermoneutral zone (Buffenstein and Jarvis in press) permit employment of torpor at the high ambient temperatures encountered in the plugged burrows. Under these circumstances, savings in energy and water occur whilst still allowing full control of co-ordination and awareness of changes in its environment whereas at lower temperatures, savings are greater but at the expense of co-ordination.

Field burrow temperatures are insufficient in that these were only obtained in August 1980 and it is not certain how these temperatures vary throughout the year. The degree of fluctuation is, however, thought to be slight in view of the small amplitude (2-6°C) in monthly air temperature (Gourou, 1970) and the minimal effect of the far larger diel temperature range on measured burrow temperatures (pers. obs.). Twenty-four hour torpor runs were only monitored at 24°C, the acclimated laboratory temperature. However, expected percentage savings at different resting (burrow) temperatures can be estimated from minimal resting rates of coenothermic gerbils taken from Buffenstein and Jarvis (in prep.) and from minimal torpid rates at different ambient temperatures. In order to calculate the percentage saving during resting (Table 4), it is assumed that torpid and resting gerbils remain in the burrow for the same length of time. At acclimated laboratory temperatures (24°C) savings of 80.8% of the energy used during normothermia were found. The saving in energy expenditure declines as ambient temperature increases (Table 4). It is, however, still an

TABLE 4 Estimated percentage savings incurred by using torpor at different temperatures

Temperature °C	Coenothermic resting rate ($m\ell$ $O_2.g^{-1}.h^{-1}$)	Torpid resting rate ($m\ell$ $O_2.g^{-1}.h^{-1}$)	Saving during resting (%)
24	0.63	0.50	80.8
27	1.99	0.62	69.1
28	1.78	0.65	63.4
29	1.56	0.69	55.8
30	1.35	0.73	46.2
31	1.14	0.76	33.1

appreciable saving when compared to coenothermic energy expenditure.

ENTRY AND AROUSAL

Entry into torpor is merely a passive process, requiring no special mechanism for increased heat loss. It simply results from the cessation of any thermoregulatory increase in oxygen consumption below the lower critical limit of the thermoneutral zone (32°C).

The cue for arousal appears to be incorporated within a persistent circadian rhythm. During arousal thermal conductance is made minimal, shivering occurs and oxygen consumption markedly increases. Heat production therefore exceeds heat loss and body temperature increases.

Rates of warming in _G. pusillus_ are high, falling within the range observed in _Microdidops pallidus_ (15g) (Bartholomew and MacMillen, 1961), but are approximately three times the rate found in the larger (30g) _Mus musculus_ (Hudson and Scott, 1979). The high rates of increase in body temperature during arousal in _G. pusillus_ may be correlated with the high rate of heat transfer in a small sized body (Table 5).

TABLE 5 Arousal rates and mass in several torpid animals

Species	Mass g	Critical TB °C	Maximum rate of arousal °C/min.	Source
Citellus tereticaudus	230	-	0.25	Hudson & Bartholomew, 1964
Citellus mohavensis	200	-	0.40	Bartholomew & Hudson, 1960
Perognathus hispidus	40	10	0.47	Wang & Hudson, 1970
Peromyscus boylei	32	18	0.42	Morhardt, 1970
Mus musculus	30	16	0.26	Hudson & Scott, 1979
Peromyscus leucopus	24	17	0.54	Morhardt, 1970
Peromyscus eremicus	24	19	0.64	Morhardt, 1970
Perognathus californicus	20	15	0.67	Tucker, 1962
Microdidops pallidus	15	-	0.80	Bartholomew & MacMillen, 1961
Crocidura russula	14	19	0.90	Nagel, 1977
Gerbillus pusillus	13	20	0.80	Present study
Crocidura leucodon	12	19	0.90	Nagel, 1977
Baiomys taylori	6	22	-	Hudson, 1965
Pipistrellus hesperus	4	-	1.02	Bartholomew *et al.*, 1957
Suncus etruscus	2	19	2.00	Nagel, 1977

Oxygen consumption during arousal of torpid G. pusillus reaches a maximal rate approximately two hours after the commencement of arousal. The observed rates of increase in body temperature are greater than can be accounted for by minimal heat loss and maximal heat production and it is probable that during arousal, G. pusillus depends in part on an anaerobic release of energy and acquires an oxygen debt. Use of anaerobic metabolism has been reported frequently (Bligh, 1973; Hill, 1976). During arousal aestivators have been shown to have less pronounced maximal oxygen consumption peaks than hibernators (Hudson, 1973). In fact an oxygen overshoot during arousal has not been observed in G. pusillus or in Peromyscus sp. (Hudson, 1965; Morhardt, 1970), suggesting that the overall rate of heat production is more finely tuned to the requirements of heating the body in these animals. After peaking, the rate of oxygen consumption drops slightly and is then maintained at coenothermic levels. The duration of this coenothermic state is dependent on the availability of food. If no food is available G. pusillus rapidly re-enters torpor (Fig. 5).

EFFECT OF TEMPERATURE ON OXYGEN CONSUMPTION

Oxygen consumption during torpor, as expected, was found to be temperature dependent. Rectal temperature was a more accurate index of oxygen consumption than ambient temperature, primarily because the depth of torpor at any one ambient temperature was variable. The deepest torpor occurred at the lowest ambient temperature (15°C) monitored, the lowest rectal temperature at this temperature was 16.7°C (Fig. 10). At this temperature, oxygen consumption was minimal and co-ordination poor. *Gerbillus pusillus* could not right itself nor rouse when handled. Similar responses to low temperatures have been observed in *Peromyscus sp.* and *Dipodomys microps* (MacMillen, 1972; Breyen *et al.*, 1973).

Extrapolation of the equation relating torpid oxygen consumption to body temperature cuts the abscissa at 15.2°C and death would most likely occur at that body temperature. Hudson and Eller (1974) have found in the white-footed mouse that the heart starts malfunctioning between 15 and 16°C and death results from vascular inco-ordination (Webb *et al.*, 1969).

The response to low temperatures in *G. pusillus* is merely of academic interest for such low temperatures would not normally be encountered in its micro-environment. That they survived these low ambient temperatures and body temperatures reflects their tolerance to a vast range of temperatures and their inherent ability to survive short periods of the most unfavourable conditions.

CRITICAL AROUSAL TEMPERATURE

MacMillen (1965) defines critical arousal temperature as the body temperature below which torpid animals are no longer capable of active arousal without the external application of heat. There appears to be no direct relationship between body mass and the critical arousal temperature (Table 5). Gerbillus pusillus, like many other small rodents, could not arouse without an exogenous heat supply when body temperature was less than 20°C. It is most unlikely that burrow temperatures for G. pusillus would fall below this value, especially in the dry season when G. pusillus would most probably employ energy-conserving torpor. An adequate safety margin therefore exists ensuring that G. pusillus, in the wild, would be able to spontaneously arouse out of torpor.

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CHAPTER 4

Energy and water balance during torpor and hydropenia in the pigmy gerbil, Gerbillus pusillus.

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Running title: Energetics of torpor in G. pusillus

SUMMARY

Under *ad lib.* food conditions, *G. pusillus* used 107% of the predicted daily energy expenditure. This increased significantly with water deprivation to 116% of the allometric expected value, thereby reflecting an increase in activity in search of food with high moisture content, a shift to metabolic water for meeting the animal's water requirements and a change in the state of hydration of the animal. Economic water expenditure through efficient kidney concentrating ability, reduced pulmocutaneous evaporation, reduced faecal water loss and tolerance to haemoconcentration, was sufficient to impart virtual independence of exogenous water.

Gerbillus pusillus responded to food shortage by abandoning homeothermy. In doing so, it was able to maintain a fairly stable body mass by monitoring energy intake and ensuring that energy expenditure did not exceed intake. There was no significant difference in energy expenditure between gerbils on a restricted energy intake and *ad lib.* water and those gerbils on a restricted energy intake and no water. Both these experimental groups were able to maintain a positive water balance, for whilst less metabolic water was available, water loss primarily through evaporation

decreased concomitantly with reduced body temperature. In addition, the volume of urine excreted when torpid accounted for approximately 5% of the volume excreted by coenothermic rodents deprived of free water. Urine, although less concentrated than that of non-torpid gerbils deprived of water, was ten times more concentrated than the plasma.

Daily torpor, although uniquely suited to energy conservation, is not without cost. A reduced body temperature resulted in a decline in 'apparent assimilation efficiency' (AE). It seems therefore that the cost of maintaining an elevated body temperature for the full duration of digestion is impractical. The cost of employing torpor as calculated from the reduced AE of food (0.5kJ.day $^{-1}$), was however insignificant in comparison to the savings accrued (32.25 kJ.day $^{-1}$) by the use of torpor.

Introduction

The regime of temperature and humidity to which burrow-dwelling nocturnal desert rodents are subjected is similar to that of mesic habitats (Kenagy, 1973). The severity of a desert environment lies not in the direct effects of heat and aridity on the bodies of small mammals; for example the maximum temperatures encountered fall well within the tolerance range for G. pusillus (Buffenstein and Jarvis, in prep.). It is rather the effects of these parameters on the availability and quality of the primary food source that stress the inhabitants of this environment. Under arid conditions, plant material in certain seasons may have low moisture contents and be very scarce. Starvation and dehydration at these times may become critical. Maximum utilization of available food and water coupled with reduced energy expenditure and water loss would therefore be advantageous for survival.

Gerbillus pusillus lives in an environment where the mean annual temperature is above 27 °C and the mean annual amplitude (ie the difference between the hottest and coldest month) ranges from 2-6 °C (Gourou, 1970). Whilst the temperature range in this environment is stable, rainfall is irregular and unreliable, varying by as much as 250% from year to year (Barkham and Rainy, 1976). Consequently vegetation is sparse and food sources are scattered and unpredictable. *Gerbillus pusillus* adaptively reduces oxygen consumption by employing torpor when food and water are severely limiting (Buffenstein, in prep.). The effect of reduced food and water supply, and the commonly associated decreased body temperature, on AE and utilization seems to have been overlooked in the past. No-one appears to have examined these criteria in hypothermic rodents. Data for torpid animals were usually excluded from energetic measurements (eg. Kenagy, 1973). The only paper dealing with energetics in torpid rodents using the 'feeding trial' method (French, 1976) assumes 'apparent assimilation efficiency' in granivorous rodents undergoing torpor to be the same as that under conditions of *ad lib.* food and water.

This study examines whether this premise is valid for *G. pusillus*, whilst also examining its energy and water requirements under conditions of *ad lib.* food and water, when deprived of water in the presence of an *ad lib.* supply of food and when food is restricted under both water treatments.

Methods and materials

Fifteen G. pusillus were housed individually in an air-conditioned laboratory (22 ± 3 °C) with a 12-hour photoperiod for four weeks, prior to experimental treatments. During the experimental runs, the sand substrate was removed so as to keep the food and faeces uncontaminated.

Millet is a well balanced food, containing approximately 3.5% fat, 12.7% protein, 80.0% total carbohydrate and 1% fibre of the dry mass (Ockerman, 1978). Micronutrients account for the remaining portion. In the present investigation 1g of millet yielded 20.88kJ. Preformed water constituted 9% of the initial mass. Assuming 0.03ml water are liberated per kilojoule metabolized (Schmidt-Nielsen, 1975), 1g millet yields 0.626 mls of oxidative water.

For the first twelve days of the experiment, food and water were supplied ad lib. Water was gradually reduced by removing water bottles and supplying all exogenous water in the form of green vegetables, and reducing the daily ration of this water source to zero over eight days. During this period no attempt was made to measure daily energy expenditure and only changes in body mass were monitored. Thereafter no free water was provided. Energy exchange and water balance were monitored when food and water were supplied *ad lib.* and again after the mass of the gerbils had stabilized during water deprivation (approximately two weeks). Animals were weighed daily, on a Mettler portable balance to the nearest 0.01g. Data per gram animal weight were calculated using the average animal weight over the duration of the experimental treatment.

Food restriction

The monitoring of energy and water was repeated when food was limited to $0.5g.day^{-1}$. Animals were maintained on this restricted diet for one week before determining the energy and water balances. Both gerbils maintained on an *ad lib.* supply and those that were deprived of water for more than six weeks were subjected to a restricted food supply.

During the week of acclimation to a restricted energy intake, rectal temperatures were regularly monitored, by inserting a copper-constantan thermocouple approximately 1cm into the rectum. This thermocouple was attached to a calibrated digital display. Unfortunately the gerbils would arouse on handling. Therefore, during the period of monitoring energy and water expenditure, a thermocouple was gently placed beneath each gerbil when resting. The thermocouples were connected to a data logger (Esterline Angus PD2064) which recorded these temperatures at half-hourly intervals whilst the gerbils were resting.

Daily energy intake (DEI)

The DEI was determined gravimetrically from the rates of food consumption and faecal production. Food consumption was measured by initially supplying a known quantity of golden millet greatly in excess of the gerbils requirements. Remaining food and husks were collected and weighed after six and twelve days. In rodents maintained on a restricted intake, weighed amounts of food were given daily. Any remaining seeds, husks and faeces were collected after six days of monitoring. Control samples of millet were monitored for any weight changes and these were then corrected for in the results. Faecal production was assessed by collecting all the faeces produced during the monitored periods. The energy content of the food and faeces was measured by microbomb calorimetery. Daily energy intake was calculated using the following equation:

$$DEI = GEI - TFE$$

where: DEI is the daily energy intake, GEI is the gross energy intake (mass of food eaten x energy provided by 1g food), TFE is total faecal energy (mass of faeces x energy content of 1g of faeces).

Urine energy content was ignored in these calculations. It has been found to constitute a negligible fraction of energy exchange (see Grodzinski and Wunder, 1975).

'Apparent assimilation efficiency' (AE) was calculated from the daily energy intake (DEI) and the gross energy intake (GEI):

AE = DEI/GEI x 100 (Grodzinski and Wunder, 1975)

Daily energy expenditure (DEE)

With food _ad lib._, biomass production was assumed to be zero because all gerbils were non-breeding adults and they were monitored only when their weights were stable (mass change <0.1%). Daily energy expenditure therefore represented only respiration required for body maintenance and activity and under these conditions was equal to daily energy intake (DEI).

When food intake was restricted, mass decreased slightly and it was assumed that the changes represented the catabolism of fat reserves. Therefore, DEE was calculated by including the energy content of mobilized fat ($23.36 kJ.g^{-1}$, Jagosz _et al._, 1979; Withers, 1982).

Maximum rate of passage of seed.

Maximum rate of passage of seed was roughly determined by supplying G. pusillus with seed that had been dyed blue with baking food colouring. Dyed seed was supplied for three hours (6-9pm), thereafter the blue seeds were replaced with undyed seeds. Faeces were collected at two hour intervals and their colour observed. The maximum rate of passage was assumed to be the time taken for the first dyed faeces to occur. The minimum rate was estimated from the last appearance of observed dyed faeces.

Water Monitoring

All acclimated gerbils, whether maintained on an ad lib. or restricted diet, were subjected to a sequence of two different water regimes: (i) an ad lib. supply (ii) the withholding of all exogenous water (hydropenia). Urine, faeces and 200µl of blood were collected from each animal after six and twelve days of each experimental water treatment.

Water intake was determined by weighing the drinking bottles initially and again at the end of each six-day monitoring period. Control bottles were kept so as to enable correction for water loss due to evaporation and handling. Preformed water in the seeds was determined by drying known quantities of seed at 60 °C to constant mass. Metabolic water was calculated assuming 0.03ml water.kJ $^{-1}$ of energy expended, (Schmidt-Nielsen, 1975).

Faecal water loss was determined by measuring the faecal water content in freshly voided faeces, produced whilst handling the gerbils. Faeces were stored individually in weighed small microvials and weighed as soon as possible on an electronic microbalance to the nearest 0.01mg. Faeces were then dried at 60 °C to constant mass and reweighed.

Water loss through urine was determined by collecting 24-hour urine samples under light liquid paraffin. The total volume of the urine excreted was measured by weighing the urine and a separate 10µ aliquot from the sample, so converting mass into volume.

Concentrating capacity was examined by monitoring changes with the experimental treatments in: osmolality (using a vapour pressure osmometer) and electrolytes (standard flame photometry). This was compared to concentrations in the blood. Blood samples of 200µl were taken from the canthal sinus on the anterio-dorsal aspect of the orbit, according to the method of Halpern and Pacaud (1951). These samples, collected in heparinised capillary tubes, were centrifuged and haematocrit measurements taken before the plasma was separated and frozen in sealed capillary tubes for analysis.

Pulmocutaneous water loss was not determined directly but was estimated from the water balance equation, based on the assumption that water intake (WI) is equal to water loss (WL):

$$WI = D + P + M = WL = F + U + E$$

where D = amount drunk, P = preformed water in the seeds, M = water of oxidation of energy source, F = faecal water loss, U = urinary water loss and E = evaporative water loss. Therefore

$$E = WI - (F + U)$$

At the end of the experimental period all gerbils were killed and their kidneys removed. One kidney from each animal was fixed in 10% formal saline, embedded in paraffin wax, sectioned at 7-10μ and stained with PAS and haematoxylin. This staining technique accentuates the corticomedullary boundary.

Mid-sagittal sections were placed in a negative holder of a photographic enlarger and the image projected onto paper. The outline of the organ and the corticomedullary junction were traced onto the paper at a magnification of approximately 20. The cortical and medullary areas were carefully cut out and weighed.

The relative medullary area (RMA) was determined as the ratio of these two weights. Expected maximal urine concentrating ability was calculated from Brownfield and Wunder's (1976) equation:

Maximum urine concentration ($mOsm.l^{-1}$) = 837 + 2106 RMA

Statistical analyses included student t-tests and paired t-tests where applicable (Zar, 1974). Data were considered statistically significant at $p \leq 0.05$. Unless otherwise stated mean values and standard errors are given.

Results

Gut-transit

Maximum rate of passage of dyed millet was found to be 3-4 hours. However, there was considerable variability in the rate of passage, with stained faeces still appearing some 12 hours after removal of the dyed food.

Energy balance

No significant difference in energy balance was observed between the sexes. Similar findings have been reported by several workers in animals where sexual differences in size are negligible (Mele, 1972; Mazen and Rudd, 1980; Framstad *et al*., 1981). Pooled data were therefore used.

The DEE under conditions of *ad lib*. food and water was 107% of that predicted by mass. Rate of food consumption and DEE (Table 1) did not alter with hydropenia ($p \geq 0.10$). The deviation from the allometric predicted value, however, increased to 116% when deprived of water. When food was restricted, water deprivation did not significantly ($p \geq 0.05$) alter DEE or the AE (Table 2). All gerbils subjected to this regime for more than three days showed daily torpor. The energy content of the faeces voided when torpid was significantly greater than when coenothermic ($p \leq 0.001$). This resulted in a significantly lower ($p \leq 0.02$) AE (Table 2) than that observed when coenothermic.

TABLE 1 Energy balance for coenothermic *Gerbillus pusillus* when provided with *ad lib.* water (+H_2O) and when deprived of water (-H_2O)

	+H_2O		-H_2O	
	$\bar{X}$	S.E.	$\bar{X}$	S.E.
Number of animals	9		9	
Average mass (g)	13.35	0.71	12.57	0.49
Food consumption (g.day^{-1})†	1.69	0.06	1.84	0.12
Faecal production (g.day^{-1})†	0.13	0.01	0.11	0.01
Energy content of faeces (kJ.g^{-1})†	16.09	0.36	16.49	0.09
GEI (kJ.day^{-1})	35.28	1.15	36.04	1.13
Faecal energy (kJ.day^{-1})	1.99	0.16	1.80	0.16
DEE (kJ.day^{-1})	33.29	1.08	34.24	1.11
% predicted DEE *	107.36	1.03	115.90	1.68
Apparent assimilation efficiency (%)	94.51	0.29	95.04	0.42

† Data are expressed per gram dry weight

* Calculated from Grodzinski and Wunder (1957) equation for a granivorous rodent, converted to kJ and corrected for temperature according to Morrison and Ryser (1951)

Predicted DEE at 22°C (kJ.g^{-1}day^{-1}) = $8.441 \times M(g)^{-0.50}$

TABLE 2 Energy balance for *Gerbillus pusillus* undergoing torpor, when provided with *ad lib.* water (+H_2O) and when deprived of water (-H_2O)

	+H_2O		-H_2O	
	$\overline{X}$	S.E.	$\overline{X}$	S.E.
Number of animals	5		4	
Average mass (g)	12.03	0.67	11.50	0.68
Mass change (g.day^{-1})	-0.07	0.03	-0.03	0.02
Food consumption (g.day^{-1})⌿	0.42	0.03	0.44	0.02
Faecal production (g.day^{-1})⌿	0.04	0.01	0.03	0.00
Energy content of faeces (kJ.g^{-1})⌿	18.49	0.47	18.02	0.45
GEI (kJ.day^{-1})	8.72	0.68	9.34	0.38
Faecal energy (kJ.day^{-1})	0.72	0.06	0.63	0.06
Fat mobilization (kJ.day^{-1})	1.75	0.62	0.74	0.40
DEE (kJ.day^{-1})	9.76	0.74	9.45	0.22
% Predicted DEE *	33.64	3.22	32.65	0.53
Apparent assimilation efficiency	91.48	1.20	92.25	0.94

⌿ Data are expressed per gram dry weight

* Calculated from Grodzinski and Wunder (1957) equation for a granivorous rodent, converted to kJ and corrected for temperature according to Morrison and Ryser (1951)

Predicted DEE at 22°C $(\text{kJ.g}^{-1}\text{day}^{-1}) = 8.441 \times M(g)^{-0.50}$

Water balance

As mass had stabilised prior to monitoring water balance in hydropenic animals, it is most unlikely that water from dehydration contributed to the water balance. All parameters of water loss declined significantly when coenothermic G. pusillus was deprived of water (Table 3). Faecal water loss declined by 25% ($p \leq 0.05$) as the percentage of faecal water content decreased with water deprivation. Faecal water loss when food was limited accounted for 9% of the total water loss (TWL). This proportion of the TWL was similar to when food was abundant (8%).

Estimated evaporative water loss when food was freely available decreased significantly with hydropenia. However, the percentage of the TWL through this channel increased as the proportion lost through micturition declined markedly. When the food supply was also restricted, pulmocutaneous evaporative water loss accounted for 33% of the amount lost when food was not limiting and urine production declined to 9% of the urine volume under conditions of ad lib. food and no exogenous water (Table 4).

Decreased urine volume in non-torpid gerbils is reflected in increased urine concentrations and urine/plasma ratios (Table 5). Whilst torpid gerbils

TABLE 3 Water balance for coenothermic *Gerbillus pusillus* when provided with *ad lib.* water ($+H_2O$) and when no exogenous water is supplied ($-H_2O$)

	$+H_2O$		$-H_2O$		
	$\bar{X}$	S.E.	$\bar{X}$	S.E.	SIG*
Number of animals	9		9		
Mass (g)	13.35	0.71	12.57	0.49	NS
% Faecal water	51.11	0.85	47.03	0.66	HS
Water intake					
Free water drunk ($ml.day^{-1}$)	0.80	0.15	-	-	
Preformed water ($ml.day^{-1}$)$^{+}$	0.15	0.01	0.17	0.01	NS
Metabolic water ($ml.day^{-1}$)$^{\not+}$	0.99	0.03	1.03	0.03	NS
Total intake ($ml.day^{-1}$)	1.94	0.17	1.20	0.04	HS
Water loss					
Faecal ($ml.day^{-1}$)	0.13	0.01	0.10	0.01	S
Urine ($ml.day^{-1}$)	0.51	0.07	0.18	0.02	HS
Evaporative ($ml.day^{-1}$)$^{\varnothing}$	1.30	0.13	0.92	0.03	HS
Total loss ($ml.day^{-1}$)	1.94	0.17	1.20	0.04	HS

* SIG S = Significant ($p < 0.05$) : HS = Highly significant ($p < 0.01$)
: NS = Not significant ($p > 0.10$)

$+$ Water content of millet seed was 0.09 $ml.g^{-1}$

$\not+$ 1kJ of energy expended liberates 0.03 ml water (Schmidt-Nielsen 1975)

$\varnothing$ Estimated by subtracting faecal and urinary water loss from total water intake

TABLE 4 Water balance for *Gerbillus pusillus* undergoing torpor when provided with *ad lib.* water (+H_2O) and when no exogenous water is supplied (-H_2O)

	+H_2O		-H_2O		
	$\bar{x}$	S.E.	$\bar{x}$	S.E.	SIG*
Number of animals	5		4		
Mass (g)	12.03	0.68	11.50	0.68	
% Faecal water	50.52	0.72	47.18	0.64	S
Water intake					
Free water drunk (ml.day^{-1})	0.11	0.01	-	-	
Preformed water (ml.day^{-1})$^{+}$	0.04	0.00	0.04	0.00	NS
Metabolic water (ml.day^{-1})$^{\neq}$	0.29	0.02	0.28	0.01	NS
Total intake (ml.day^{-1})	0.44	0.02	0.32	0.01	HS
Water loss					
Faecal (ml.day^{-1})	0.04	0.01	0.03	0.00	NS
Urine (ml.day^{-1})	0.02	0.00	0.01	0.00	S
Pulmocutaneous (ml.day^{-1})$^{\emptyset}$	0.38	0.02	0.29	0.01	S
Total loss (ml.day^{-1})	0.44	0.02	0.32	0.01	HS

* SIG S = Significant ($p<0.05$) : HS = Highly significant ($p<0.01$)
: NS = Not significant ($p>0.10$)

+ Water content of millet seed was 0.09 ml.g.$^{-1}$

≠ 1kJ energy expended liberates 0.03 ml water (Schmidt-Nielsen 1975)

ø Estimated by subtracting faecal and urinary water loss from total water intake excreted significantly smaller volumes of urine than coenothermic gerbils, urine concentration was approximately one third of that excreted by hydropenic gerbils with an _ad lib._ supply of water. Plasma concentrations and haematocrit readings also increased with water deprivation (Table 5). This was most pronounced in non-torpid hydropenic gerbils.

Kidney morphology

Relative medullary area was 1.666 ± 0.053 (n=15). Predicted maximum concentration, using Brownfield and Wunder's (1976) equation, would therefore be 4346 mOsm. This is in fact slightly higher than concentrations obtained (Table 5).

TABLE 5 Urine and blood properties of *Gerbillus pusillus* under different dietary and water regimes

	$+H_2O$		$-H_2O$		SIG*
	$\overline{X}$	S.E.	$\overline{X}$	S.E.	
			UNRESTRICTED FOOD		
Number of animals	8		8		
Haematocrit (%)	54.3	0.7	58.1	0.8	S
Plasma (mOsm)	440.1	20.1	520.4	20.6	S
Plasma Na (mM)	191.3	8.3	202.3	10.5	NS
Plasma K (mM)	7.4	0.9	12.6	1.9	S
Urine (mOsm)	1759.0	202.6	3974.3	86.7	HS
Urine Na (mM)	8.3	0.9	12.1	3.2	NS
Urine K (mM)	126.5	20.2	291.1	15.6	HS
			RESTRICTED FOOD		
Number of animals	6		6		
Haematocrit (%)	53.6	0.4	54.0	1.0	NS
Plasma (mOsm)	416.0	29.9	463.0	28.6	NS
Plasma Na (mM)	172.0	10.7	188.7	10.3	NS
Plasma K (mM)	13.7	1.9	11.8	2.7	NS
Urine (mOsm)	1311.0	123.0	2530.0	293.4	HS
Urine Na (mM)	15.3	6.2	18.8	5.3	NS
Urine K (mM)	127.2	2.5	198.3	24.8	S

SIG* S = Significant ($p<0.05$) : HS = Highly significant ($p<0.01$)

NS = Not significant ($p>0.10$)

Na is the sodium cation concentration and K is the potassium cation concentration.

Discussion

Energy Balance

The daily energy expenditure of G. pusillus determined by feeding trial methods was 10% greater than that determined by respirometry (Buffenstein, in prep.). McNab (1963) suggested that feeding trial energy determination was a more reliable assessment than oxygen consumption. Laboratory measurements of DEE using this method must be an underestimate, for no time is spent on energy-consuming activities like searching for food, digging, defending territories or avoiding predators. Several workers have nevertheless found close agreement with field measurements using D_2O^{14} and laboratory assessments (Mullen and Chew, 1973; Johnson and Schreiber, 1979). Both laboratory methods of determining DEE (Buffenstein, in prep. and the present investigation) were within 10% of the allometric predicted value for granivorous rodents. Unfortunately no field stomach contents of G. pusillus were collected. From the stomach content data of Jarvis (pers com.), this gerbil is like most other desert rodents (Reichman et al., 1979), opportunistic in its feeding habits but primarily granivorous. Granivorous desert rodents typically have high digestive efficiencies (Johnson and Groepper, 1970; Schreiber, 1979). Gerbillus pusillus is no exception with an AE approaching a physiological maximum (95%).

The AE did not alter with water deprivation. The percentage predicted DEE increased significantly ($p \leq 0.05$), once body weight had stabilised at 94% of the original body mass. Whilst this increase in DEE might reflect increased searching activity for succulent food or could result from increased dependence on metabolic water for meeting the gerbil's water requirements, it may indeed be merely an artifact caused by the change in hydration state in the animal. Increased plasma concentrations and elevated haematocrits indicate that the gerbils had become dehydrated. Despite the fact that these animals could survive indefinitely without exogenous water and that mass had stabilised prior to monitoring the effect of hydropenia on DEE, body mass of gerbils deprived of water obviously did not accurately reflect the amount of metabolising tissue. The DEE expressed per animal did not alter significantly ($p \geq 0.10$) with the two water treatments, suggesting that changes in DEE may be best accounted for by dehydration.

When food was restricted to 0.5g of millet per animal per day, <u>G. pusillus</u> could not maintain a positive energy balance without abandoning strict homeothermy. By controlled use of torpor, however, these gerbils could markedly reduce weight loss. Delany and Happold

(1979) however suggested that torpor was generally uncharacteristic of tropical small mammals. *Gerbillus pusillus*, however, encounters periods when food and water may be limiting. Employment of torpor under these circumstances is common (Tucker, 1966; Brown and Bartholomew, 1969; Brower, 1970; Hainsworth *et al.*, 1977; Reichman and Brown, 1979).

No significant difference was found between gerbils on a restricted food intake with an *ad lib.* supply of water and those on a restricted food intake that had been water deprived. This implies that it is limited food supply rather than water that determines the duration of hypothermia. Rodents rarely exhibit daily torpor when food is abundant, suggesting that the use of torpor is an emergency strategy ensuring survival when food is critically limiting. At other times this energy conserving mechanism is not favoured, implying some selective cost associated with being torpid. Torpidity is known to impede an animal's response to predators and to rapid changes in the environment. In addition the amount of time spent foraging or mating is also reduced (Reichman and Brown, 1979). However, no previous reference has been made to decreased digestive efficiency. Faecal energy content increased significantly ($p \leq 0.001$) when the gerbils underwent daily torpor, suggesting that when food is scarce there is a significant decrease in AE. This at first appears to be anomalous for surely it would be more advantageous to obtain the maximum amount of energy and nutrients from the limited food available. Although coprophagy was not observed in the laboratory, it is a common phenomenom in rodents (Howell and Gersh, 1935; Kalugin, 1974; Kenagy and Hoyt, 1980). Eating of the energy-rich faeces during arousals may possibly occur, enabling use of this otherwise lost energy source. A reduction in enzyme activity at the lower body temperature might account for the observed decrease in AE. Whilst this decline is statistically significant it is small. It is therefore not possible to assign biological meaning to this decline. However one can hypothesize that it is significant in view of the high energetic cost of maintaining constant body temperature. The energetic cost of maintaining coenothermia for the full duration of digestion (as estimated from the rate of gut-transit of dyed faeces to be approximately four hours) is between 46 and 55% of the total daily energy intake (calculated from oxygen consumption rates of 4.06 $mlO_2.g^{-1}.h^{-1}$ and 5.04 $mlO_2.g^{-1}.h^{-1}$ in Buffenstein, in prep.). Whilst mammals always use most of their energy expenditure on temperature control, when food is limiting the cost of temperature regulation becomes prohibitive. The concomitant decline in AE and thus the cost of employing torpor (0.05kJ.day^{-1}) is insignificant in comparison to the savings (32.25kJ.day^{-1}) accrued.

Employment of torpor is therefore preferable to the maintenance of a constant body temperature for the full duration of digestion.

If environmental conditions become as severe as the experimental treatment, the energy loss from increased activity and thermoregulation may outweigh any gain in leaving the confines of the burrow in search of food. Literature on optimal foraging behaviour suggests that organisms should evolve to maximise the net rate of energy intake while foraging (see Pyke _et al._, 1977 and Reichman, 1981 for reviews). Such behaviour would require the ability to assess intake and expenditure. The precise relationship found between the duration of torpor and the energy supply imply that food shortage has been a factor in the evolutionary history of _G. pusillus_.

Water balance

Water balances on the two experimental regimes with _ad lib._ food were significantly different ($p \leq 0.005$), as were the water balances on the two water treatments with a restricted food intake (Table 3 and 4). These differences resulted primarily from the absence of drinking water and the significant decline in urine volume with water deprivation.

Bartholomew (1975) developed a formulation; dietary water index, IDW, for quantifying the water gain or loss from ingested food in birds where:

$$\text{IDW} = \frac{\text{preformed water in food}}{\text{water in excreta (faeces \& urine)}}$$

This formula is based on the assumption that evaporative water loss is approximately equal to metabolic water liberated during the oxidation of hydrogen in the food. If IDW = 1 water is neither gained nor lost as a result of eating. If IDW $<$ 1 eating increases the rate of water loss and if IDW $>$ 1 eating results in a net gain of water. If data for coenothermic gerbils (Table 3 and 4) are inserted in this formulation, an IDW of 0.6 is obtained when water is restricted. It appears then, that a net loss results from eating when deprived of water with food freely available. Indeed, many birds and mammals that possess a negative IDW decrease food consumption when access to free water is witheld (Bartholomew, 1975). When food was freely available, apart from one hypothermic animal excluded from the data for this group, all gerbils consumed similar quantities of food irrespective of the water regime. This discrepancy from that predicted by the IDW may be explained by the fact that the basic assumption in this index does not hold for _G. pusillus_. When deprived of exogenous water, the quantity of water available in the equation below increases through an apparent decline in evaporative water loss.

$$M - E = F + U - P$$

where M is metabolic water, E is evaporative water loss, F is faecal water, U is the volume of urine excreted and P is the preformed water in the food.

Preformed water is highly variable and may be augmented by feeding at night when the humidity increases or by storing the seed caches in burrows where vapour pressure is maximal (Morton and MacMillen, 1982). Voluntary drinking when water was available amounted to $0.06 ml.g^{-1}.day^{-1}$. This falls within the range of reported data ($0.04-0.10 ml\ H_2O.g^{-1}.day^{-1}$) for desert rodents (Harriman, 1969; McManus, 1972). Total water intake declined significantly ($p \leq 0.01$) when the gerbils were subjected to a restricted food regime and provided with *ad lib.* drinking water. They only drank one sixth of the amount drunk when *ad lib.* food was provided. This drop can be attributed to decreased water requirements during torpor.

The ability to concentrate urine and therefore reduce the volume voided appears to be the most important factor in the water balance of *G. pusillus*. Urine volume declined by 60% when no exogenous source of water was supplied. This was coupled with a three-fold increase in urine osmolality to approximately 4000mOsm. This osmolality is similar to that found in water deprived arid-adapted *Acomys cahirinus* (Borut and Shkolnik, 1974), *Dipodomys spectabalis* (SchmidtNielsen, 1979); *Eligmodontia typus* (Mares, 1977) and *Peromyscus sp* (Dewey *et al*. , 1965). However, it is among the lower values of maximum urine osmolality for desert rodents independent of exogenous water (Table 6). This urine concentrating capacity, was nevertheless sufficient to impart virtual independence of external sources of water. Maximum urine concentration is said to be proportional to kidney structure (Brownfield and Wunder, 1976) and to the quantity of electrolytes for excretion (Harvey, 1974). In *G. pusillus* the maximum urine concentration was 8% less than predicted, suggesting that experimental conditions were not sufficiently stressful to elicit the maximum concentrating potential.

Reductions in urine output were accompanied by substantial increases in potassium cation concentration ($p \leq 0.02$) during hydropenia (from 126.5mM-291.1mM). This is indicative of an increased secretion of adreno-corticosteroids and anti diuretic hormone. Sodium electrolytes on the other hand, showed no response to water deprivation ($p \geq 0.10$). The extremely low concentration of sodium in the urine and its low

TABLE 6 Maximum urine concentration and urine/plasma ratio for rodents independent of exogenous water

Species		Urine concentration mOsm	Urine/ Plasma ratio	Source
Peromyscus critinus	N. America	3 047	12.5	MacMillen & Christopher, 1975
Dipodomys spectabalis	N. America	4 090	10.4	Schmidt-Nielsen, 1964
Gerbillus pusillus	N. Africa	4 380	8.8	Present study
Rhabdomys pumilio	Namibia	4 554	8.6	Unpublished obs.
Notomys cervinus	Australia	4 920	14.2	MacMillen & Lee, 1967
Dipodomys merriami	N. America	5 540	14.0	Schmidt-Nielsen, 1964
Gerbillus gerbillus	N. Africa	5 590	14.0	Burns, 1956
Gerbillurus tytonis	Namibia	6 324	11.6	Unpublished obs.
Jaculus jaculus	N. Africa	6 500	16.0	Schmidt-Nielsen, 1964
Notomys alexis	Australia	9 370	18.0	MacMillen & Lee, 1967

urine/plasma ratio (0.04-0.07) are indicative of an efficient counter current system whereby sodium ions are recycled (Gilles, 1979). These low concentrations are typical of arid-adapted rodents.

Torpid water-deprived gerbils excreted 4.7% of the volume of urine produced under coenothermic water deprived conditions. Similar reductions have been shown in hibernating mammals (Raths and Kulzer, 1976). This reduction is associated with a marked decline in water 'liberated' through metabolism. Although there is also a decline in the quantity of wastes to be excreted, there is still a need for water conservation. However, the need for extreme concentration may have been reduced. This is suggested by the fact that urine concentration in torpid G. pusillus was lower than in non-torpid gerbils. Fisher and Manery (1967) have presented evidence that mammalian kidney efficiency declines during hypothermia. This is a result of a decrease in glomerular filtration rate, a consequence of diminished renal blood flow during hypothermia. Lack of glomerular filtration would, however, cause osmolality to equilibrate between the renal interstitial fluid and the blood plasma and urine ought therefore to be isotonic to the plasma (Moy, 1971). This was not the case in this investigation, for although urine osmolality was lower than in coenothermic hydropenic gerbils, it was approximately ten times the concentration of the plasma, implying that the urine was formed during non-torpid periods. Decreased urine concentration in G. pusillus was, therefore, more likely to be the net result of a reduction in the quantity of excretory products and an increase in water conservation through a reduction in evaporative water loss.

Plasma concentration of non-torpid gerbils also increased significantly ($p \leq 0.02$) with water deprivation. This was reflected in elevated haematocrits. Tolerance to haemoconcentration is not uncommon in arid-adapted rodents and has been reported by Kenagy (1973); Haggag and El-Husseini (1974); Baverstock (1976); Collins (1978); Donaldson and Edwards (1981) ; Scelza and Knoll (1982). Such tolerance imparts yet another adaptation of xerophilous rodents to their environment, provided of course the blood does not become too thick to prevent normal functioning. Hypothermic gerbils showed less pronounced increases in plasma concentration with water deprivation. Sample size was however small and it is probable that the slight changes observed between torpid gerbils deprived of water and those with an ad lib. supply of water were not biologically significant. These plasma concentrations, nevertheless, indicate that water stress was not as severe, when torpor was employed.

Faecal production was found to be low when the gerbils were maintained on a high carbohydrate diet as the digestibility coefficient was high. This coupled with a significant decline in percentage faecal water content when the animals were water deprived, resulted in a very low faecal water loss (7-8%) relative to the total water loss. The few available data in the literature indicate that under conditions of water stress, faecal water loss is reduced by increased reabsorption of water in the intestine (SchmidtNielsen, 1964). The percentage faecal water content for hypothermic gerbils on ad lib. water and water deprived treatments were significantly different but were similar to normothermic gerbils subjected to the same water treatments. This suggests that torpor does not affect this avenue of water loss and it is rather the amount of water in the diet that governs faecal water loss.

Estimated pulmocutaneous water loss, in keeping with many other arid-adapted rodents (MacMillen, 1972; Reaka and Armitage, 1976; Deavers and Hudson, 1979), was significantly reduced during water deprivation. In the field pulmocutaneous water loss would be still further reduced by the high vapour pressures in the burrows. In fact Bradley and Yousef (1972) suggested that it would become insignificant when the rodent is resting in its burrow.

When food was limiting, G. pusillus lost only 33% of the pulmocutaneous evaporative water loss of individuals on an ad lib. food diet. Pulmocutaneous water losses for individuals on a limited food regime were similar, irrespective of the presence or absence of free water and were linked to torpor-related changes in ventilation, body temperature and posture. For: i) the lower the body temperature, the smaller the oxygen requirements and hence the concomitant decline in the volume of expired air; ii) the lower the body temperature, the lower the absolute water content of the expired air (Bintz and Roesbury, 1978); iii) hypothermic gerbils adopt a spheripsoid position, with the head tucked into the body. This not only reduces the surface area to the environment but also results in the gerbil breathing in a micro-environment close to the body where the humidity is high.

Most animals maintain a balance between energy intake and expenditure. This is achieved either through the control of intake or through the control of expenditure. Gerbillus pusillus is not an exception, in that under various conditions of food and/or water deprivation it can rapidly alter its energy and water expenditure to counteract these fluctuations.

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PART 3

CHAPTER 5

The importance of microhabitat in thermoregulation and thermal conductance in two Namib rodents;- a crevice dweller, *Aethomys namaquensis* and a burrow dweller, *Gerbillurus paeba*.

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Effect of microhabitat on thermoregulation

ABSTRACT

Thermoregulatory measurements of two Namib rodents; Gerbillurus paeba, a burrow dweller, and Aethomys namaquensis, a crevice dweller were compared. Both were similar to other small arid-adapted rodents in that basal metabolic rates were reduced, thermoneutral zones narrow and evaporative water losses low. Rates of conductance and thermal lability, however, at ambient temperatures below the thermoneutral zone were significantly different ($p \leq 0.01$). The rock rat A. namaquensis, living in a microclimate characterised by a large diel range and low humidities, compensates for a reduced basal metabolic rate by having a low rate of conductance. In this way it maintains precise thermoregulatory control. Gerbillurus paeba, on the other hand, living in a thermally stable milieu, does not control body temperature precisely. This animal instead utilizes a high rate of conductance to remove metabolic heat produced within the body. This would be advantageous to an animal living in a plugged burrow where the high humidities encountered impede the rate of evaporative cooling.

The energetic responses of both species, above the thermoneutral zone, appear to reflect very closely the environmental conditions which occur in the microhabitat that they rest in during the day.

Gerbillurus paeba shows less tolerance to temperature fluctuations than *A. namaquensis*, but shows more marked increases in short term cooling mechanisms at high ambient temperatures. Despite the increased use of evaporative cooling through salivation and panting in addition to pulmocutaneous evaporation, exposure to ambient temperatures above 38 °C is rapidly lethal to *G. paeba*.

Key word index:- Thermoregulation; thermal conductance; metabolic rate; evaporative water loss; crevice dweller; burrow dweller; *Aethomys namaquensis*; *Gerbillurus paeba*; Namib; desert.

INTRODUCTION

Interspersed amongst the characteristic red sand dunes of the Namib desert are gravel plains and numerous rocky outcrops called Kopjies or inselbergs (Logan, 1960). Aethomys namaquensis, the rock rat, is the predominant rodent on the rocky outcrops of the eastern side of the desert (Coetzee, 1969). Unlike most rodents in the Namib, the rock rat does not excavate burrows but rather utilizes rock crevices as a shelter from predation and intense solar radiation, leaving this sanctuary after dark to forage (Roberts, 1951).

Gerbillurus paeba, the pigmy gerbil, is the most abundant gerbil on the lower slopes and in the troughs of the sand dunes. Here, it excavates simple burrows, measuring approximately 30-40mm in diameter and 2.5m in length, to depths of approximately 20cm (De Graaff and Nel, 1965). The entrance of the burrow is plugged with sand during the day, so providing not only a shelter from predators and radiation but also a microhabitat, where changes in light, temperature and humidity, like that of gophers, are negligible (Kennerly 1964; McNab 1966).

Whilst literature on thermoregulation in rodents is generally abundant (see Hart, 1971; Mcnab, 1983 for reviews), there is a dearth of information concerning African rodents. Furthermore, whilst energetics of fossorial and semi-fossorial rodents have received much attention (Hart, 1971; Bradley and Yousef, 1972; McNab, 1979a), a comparison of the effects of microhabitat on thermoregulation and associated parameters has not been previously examined.

This paper attempts to examine whether there are significant differences in thermoregulation that may be attributed to the open crevice microhabitat of *A. namaquensis* and the sheltered burrow microhabitat of *G. paeba*.

PROCEDURE

Animals were trapped in the Namib Park near Tumasberg (23°29'S, 15°32'E), and near Gobabeb (23°34'S,15°03'E). The climate of these areas has been described by Schulze and McGee (1978).

For two months prior to the experiment, 15 *G. paeba* and 15 *A. namaquensis* were kept individually in cages floored with fine sand and containing a nest box. These cages were placed in an air conditioned room with a 12L:12D photoperiod at a temperature of 20-26°C and a relative humidity of 44-50%.

The rodents were fed an ad lib. diet of mixed bird seed. Water was provided in the form of fresh vegetables. During this period body mass was regularly monitored to the nearest 0.01g using a Mettler portable balance.

The effect of ambient temperature on body temperature, oxygen consumption and evaporative water loss were all monitored during daylight hours when the rodents are normally inactive.

Body temperature

The relationship between body temperature and ambient temperature, ranging between 12-41°C was monitored. Body temperature was monitored by inserting a copper-constantan thermocouple approximately 2cm into the rectum. This thermocouple was connected to a calibrated digital display (Bailey Bat). The rodents were given four hours to become thermally equilibrated before body temperature was recorded. At ambient temperature above 40°C, this equilibration period was reduced to 2,5 hours.

Oxygen consumption

Oxygen consumption and evaporative water loss were measured simultaneously over ambient temperatures of 12-41 °C in 15 gerbils and 15 rock rats. This was done by placing a non-fasting post absorptive rodent (i.e. one that had eaten during the scotophase but had stopped eating at least four hours prior to the commencement of the experiment), in a clear perspex respiratory chamber (75mm by 150mm) with a wire mesh platform on which the rodent rested. The chamber and a similar one without an animal (the control) were placed in a larger constant temperature and humidity chamber (ambient temperature control ± 1.0 °C, humidity control ± 2.0%). Each respiratory chamber was equipped with ports for a thermocouple and air vents. Air flowed through the respiratory chamber at 200 $cm^3.min^{-1}$ and then over a relative humidity probe (Vaisala humicap HM1-14) before being dried over silica gel and fed into an oxygen analyser (S-3A, oxygen analyser, N-37 oxygen sensor, applied electrochemistry inc.). The oxygen analyser monitored the difference in oxygen content between the two respiratory chambers. The oxygen analyser, thermocouples and relative humidity probe were connected to a data logger (Esterline Angus P.D. 2064) which was programmed to record at five minute intervals.

At each new ambient temperature the animal was allowed to equilibrate for one hour. Thereafter, oxygen consumption was monitored for at least three hours. At each ambient temperature, the lowest six readings for each animal, corrected to STP were used in calculating the post absorptive resting minimal metabolic rate. Rectal temperatures were taken at the end of each run.

Evaporative water loss.

The change in relative humidity between the air leaving the experimental chamber and the control was used to determine the evaporative water loss using the equation:

$$WL = \frac{CTA \times RH \times F \times 60}{1000 \times 100 \times M}$$

where WL is water loss (mg $H_2O \cdot g^{-1}.h^{-1}$), CTA is the mass of water in saturated air at ambient temperature, ($g.cm^{-3}$), RH is the change in relative humidity caused by the animal (%), F is the flow rate ($cm^3.min^{-1}$), and M is the mass of the mouse (g).

So as to avoid damage to the oxygen sensor, no mineral oil was placed beneath the mesh in the respiratory chamber. During the experimental run, the chamber was frequently examined through a viewing port in the outer temperature control chamber. If the rodent had roused and urinated, the run was interrupted, the apparatus cleaned and dried and left to equilibrate for 20 minutes. As most rodents urinated on handling, prior to being placed in the chamber, such interruptions were infrequent.

Dry thermal conductance

'Conductance' is the rate of dry heat transfer (i.e. excluding evaporative water loss) per unit area to or from the animal per degree temperature difference between the animal and its environment' (Dawson and Schmidt-Nielsen, 1966, p. 466).

Mean conductance between the body core and its environment was measured by the simultaneous measurement of metabolic heat, heat dissipated by evaporative water loss and the difference between body temperature and ambient temperature, using the equation:

$$C = \frac{HP - EHL}{T \times S} \quad \text{(Dawson \& Schmidt-Nielsen, 1966)}$$

where C is dry thermal conductance ($J.cm^{-2}.°C^{-1}.h^{-1}$), HP is metabolic heat production ($J.h^{-1}$) assuming $1cm^3$ oxygen is equal to 20.1J, EHL is evaporative heat loss

($J.h^{-1}$) assuming 1 mg water is equal to 2.34J, T is the temperature difference between body and ambient temperature (°C), and S is surface area of a mouse (cm^2) where $S = 10 \times \text{animal mass}^{0.67}$ (g)

Thermal conductance, measured this way, shows the capacity (summating all the individual characteristics e.g. vaso-constriction, pilo-erection, posture, etc.) of the animal concerned for heat loss through conduction, convection and radiation.

Minimal 'wet' conductance

Minimal conductance (i.e. including evaporative water loss) is calculated by the equation:

$$CM = \frac{M}{TB - TA} \qquad \text{(McNab, 1980)}$$

where CM is the rate of minimal conductance ($cm^3O_2.g^{-1}.°C^{-1}.h^{-1}$), M is the rate of oxygen consumption ($cm^3O_2.g^{-1}.h^{-1}$), TB is body temperature (°C) and TA is ambient temperature (°C).

Minimal conductance was also calculated from the slope of the graph relating oxygen consumption with ambient temperature, below the region of thermoneutrality, using McNab's (1980) correction factor.

All values are presented as means and standard errors, with the number of observations (n). Zar (1974) was consulted in calculating the linear regressions and the relevant t-tests used. A probability of less than 0.05 was taken as the level of significance.

RESULTS

Body temperature

Within the ambient temperature range from 10-33 °C, mean body temperature in A. namaquensis remains fairly constant (Table 1). Gerbillurus paeba on the other hand was more thermolabile. Body temperature was independent of ambient temperature between 25.5 and 34 °C. and was similar to that exhibited by A. namaquensis. Below 25.5 °C, its body temperature was dependent on ambient temperature and may be described by the equation;

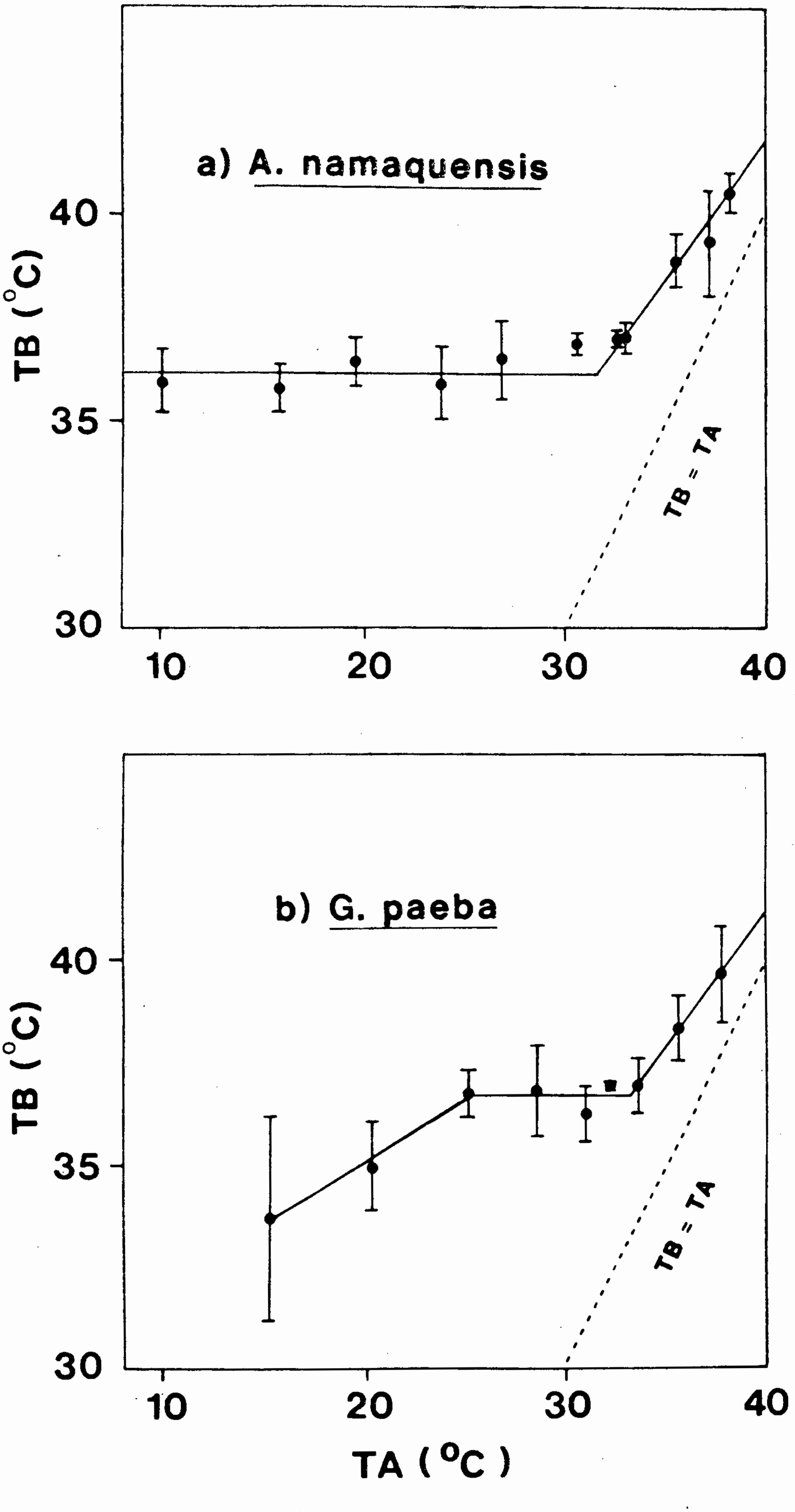
$$y = 29.08 + 0.30x \quad r = 0.99 \ (n = 6)$$

where y = mean body temperature and x = mean ambient temperature. Above ambient temperatures of 34 °C body temperature increased with increasing ambient temperature in both species (Fig. 1). Although the mean rate of increase in G. paeba (y = 11.32 + 0.76x

TABLE 1 Comparison of some aspects of thermoregulation in a crevice-dweller, *Aethomys namaquensis* and in a burrow-dweller, *Gerbillurus paeba*

	A. namaquensis		*G. paeba*	
	$\bar{x}$	S.E.	$\bar{x}$	S.E.
Mass (g)	48.37	11.64	31.13	5.28
Independent TB (°C)	36.40	0.81	36.64	0.86
BMR (mℓ $O_2.g^{-1}.h^{-1}$)	0.89	0.13	0.89	0.20
EWL (mℓ H_2O.mℓ O_2^{-1})	0.90	0.45	0.93	0.29
Cm x 10^{-1} (cm^3 $O_2.g^{-1}.h^{-1}.°C^{-1}$)	0.98	0.29	1.56	0.30
Cd x 10^{-1} at TA $<$ 30°C ($J.cm^2.h^{-1}.°C^{-1}$)	0.16	0.05	0.31	0.07
Cd x 10^{-1} at TA 38°C ($J.cm^2.h^{-1}.°C^{-1}$)	1.13	0.30	0.85	0.45
TA range in which TB is independent (°C)	10.00 - 33.00		25.00 - 34.00	
TNZ (°C)	31.60 - 34.20		33.30 - 35.60	

Figure 1 : Effects of ambient temperatures (TA) on body temperature (TB) in a) *Aethomys namaquensis* and in b) *Gerbillurus paeba*


a) A. namaquensis
TB (°C)
40
35
30
10
20
30
40
TB = TA
b) G. paeba
TB (°C)
40
35
30
10
20
30
40
TB = TA
TA (°C)

$r = 0.99$, $(n = 4)$) appears to be greater than that of A. namaquensis ($y = 15.76 + 0.64x$, $r = 0.99$, $(n = 4)$) it was not significantly different ($p \geq 0.10$).

Oxygen consumption

Aethomys namaquensis:

Oxygen consumption of A. namaquensis was minimal (0.89 ± 0.04 $cm^3\ O_2.g^{-1}.h^{-1}$) between TA 31.6 °C and 34.2 °C, so indicating a fairly small thermal neutral zone. A regression line (as shown by the line AB in Fig. 2a) fitted by the method of least squares to the data below those in the thermoneutral zone, is described by the equation:-

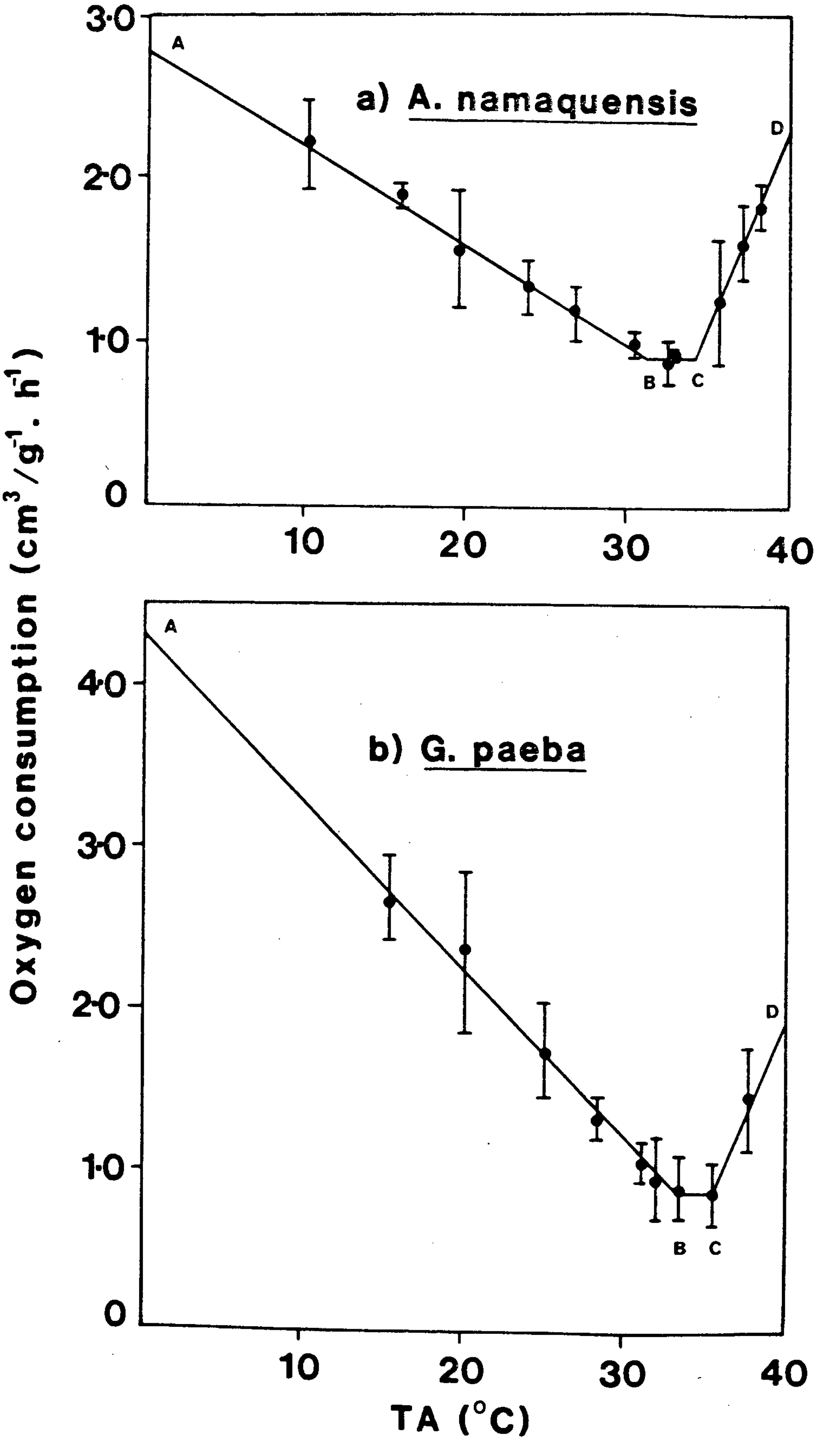
$$y = 2.780 - 0.060x \quad r = 0.85, \quad n = 49 \quad (\text{-i})$$

where (for equations (i) - (iv)) y = oxygen consumption ($cm^3O\ .g^{-1}.h^{-1}$) and x = temperature (°C). This line (i) intercepts the ordinate at 3.14 times the basic metabolic rate.

At ambient temperatures above the thermoneutral zone, the rate of oxygen consumption increased linearly (as shown by the line CD). These increases may be described by the equation:-

$$y = -7.345 + 0.241x \quad r = 0.65, \quad n = 23 \quad (\text{-ii}).$$

Figure 2 : Effects of ambient temperature (TA) on oxygen consumption in a) *Aethomys namaquensis* and in b) *Gerbillurus paeba*


a) A. namaquensis
b) G. paeba
A
B
C
D
3·0
2·0
1·0
0
4·0
10
20
30
40
Oxygen consumption (cm^3/g^{-1}. h^{-1})
TA (°C)

Gerbillurus paeba:

Oxygen consumption decreased with increasing ambient temperature between the temperature range of 15 - 30°C (Fig. 2b). This decrease in oxygen consumption (as shown by the line AB in Fig. 2b) is described by the equation below:-

$$y = 4.363 - 0.104x \quad r = 0.84, \quad n = 36 \quad (\text{-iii})$$

At ambient temperatures greater than 35°C, rates of oxygen consumption increased linearly (line CD, Fig. 2b) and may be described by the equation:-

$$y = -7.688 + 0.241x \quad r = 0.75, \quad n = 15 \quad (\text{-iv})$$

There was a fair amount of individual variability in the rates of oxygen consumption between 32 and 36°C and for this reason the zone of thermoneutrality was not easily defined. The mean rate of oxygen consumption in this range was 0.886 ± 0.200 $cm^3O_2.g^{-1}h^{-1}$; n = 24). Using the two equations describing VO_2, this value corresponds to ambient temperatures of 33.25°C and 35.64°C. It is possible that the thermoneutral zone was smaller than this range and was not accurately detected as no measurements were made at that particular temperature. Nevertheless, the measured basal metabolic rate value was 62% of that predicted by mass from Kleiber's (1975) equation.

Basal metabolic rate values (expressed as a percentage of that predicted by mass) for A. namaquensis (67.55 ± 8.33, n = 10) did not differ significantly ($p \geq 0.10$) from G. paeba (62.66 ± 13.74, n = 24). The equations relating oxygen consumption at temperatures greater than the thermoneutral zone were also not significantly different ($p \geq 0.10$) in the two species. However at temperatures below the thermoneutral zone, the slopes of the two equations (i,iii) were significantly different ($p \leq 0.01$).

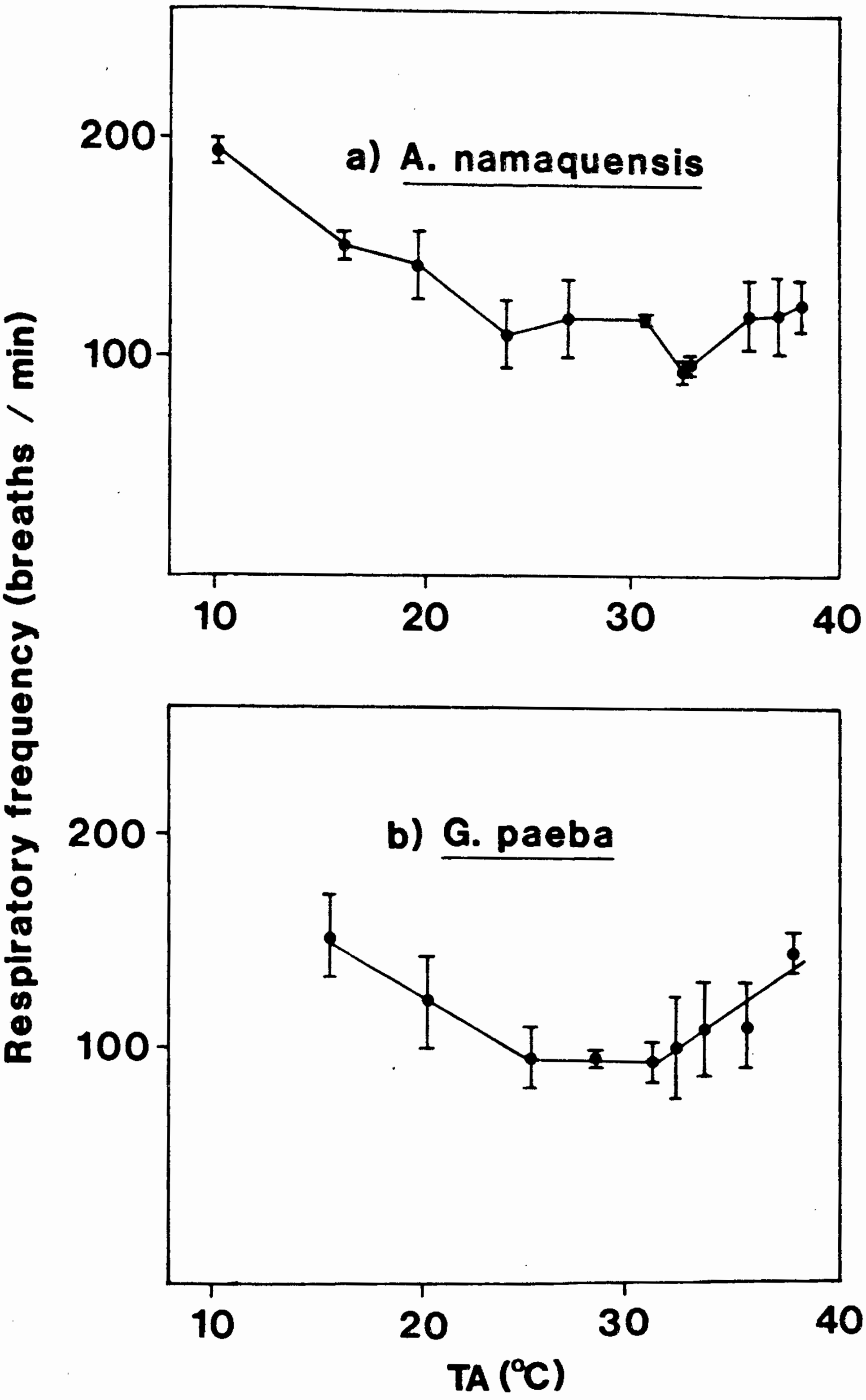
Respiratory frequency

Respiratory frequency shows similar trends to that of oxygen consumption. Below 24°C, respiratory frequency was proportional to ambient temperature in both species (Fig. 3). Respiratory frequencies at 25°C were not significantly different. However at 38°C respiratory frequency in G. paeba was significantly greater ($p \leq 0.05$), than that exhibited by A. namaquensis.

Evaporative water loss

The patterns of evaporative water loss below the region of thermoneutrality (Table 1) in both species were similar ($p \geq 0.10$). Above 33°C water loss increased considerably and individual variation was marked

Figure 3 : Changes in respiratory frequency in a) *Aethomys namaquensis* and b) *Gerbillurus paeba* with changes in ambient temperature (TA).


Respiratory frequency (breaths / min)
200
100
a) A. namaquensis
10
20
30
40
200
100
b) G. paeba
10
20
30
40
TA (°C)

(Fig. 4). Both species behaviourally increased evaporation by licking their bodies. Despite the fact that licking of fur was more pronounced in *A. namaquensis* than *G. paeba*, *G. paeba* dissipated more heat through evaporative cooling ($p \leq 0.001$), primarily through 'insensible perspiration'. At the highest ambient temperatures measured, evaporative water loss accounted for 40.1% of the total heat produced in *G. paeba*, whereas it only accounted for 25.5% of the heat produced in *A. namaquensis*.

Minimal conductance

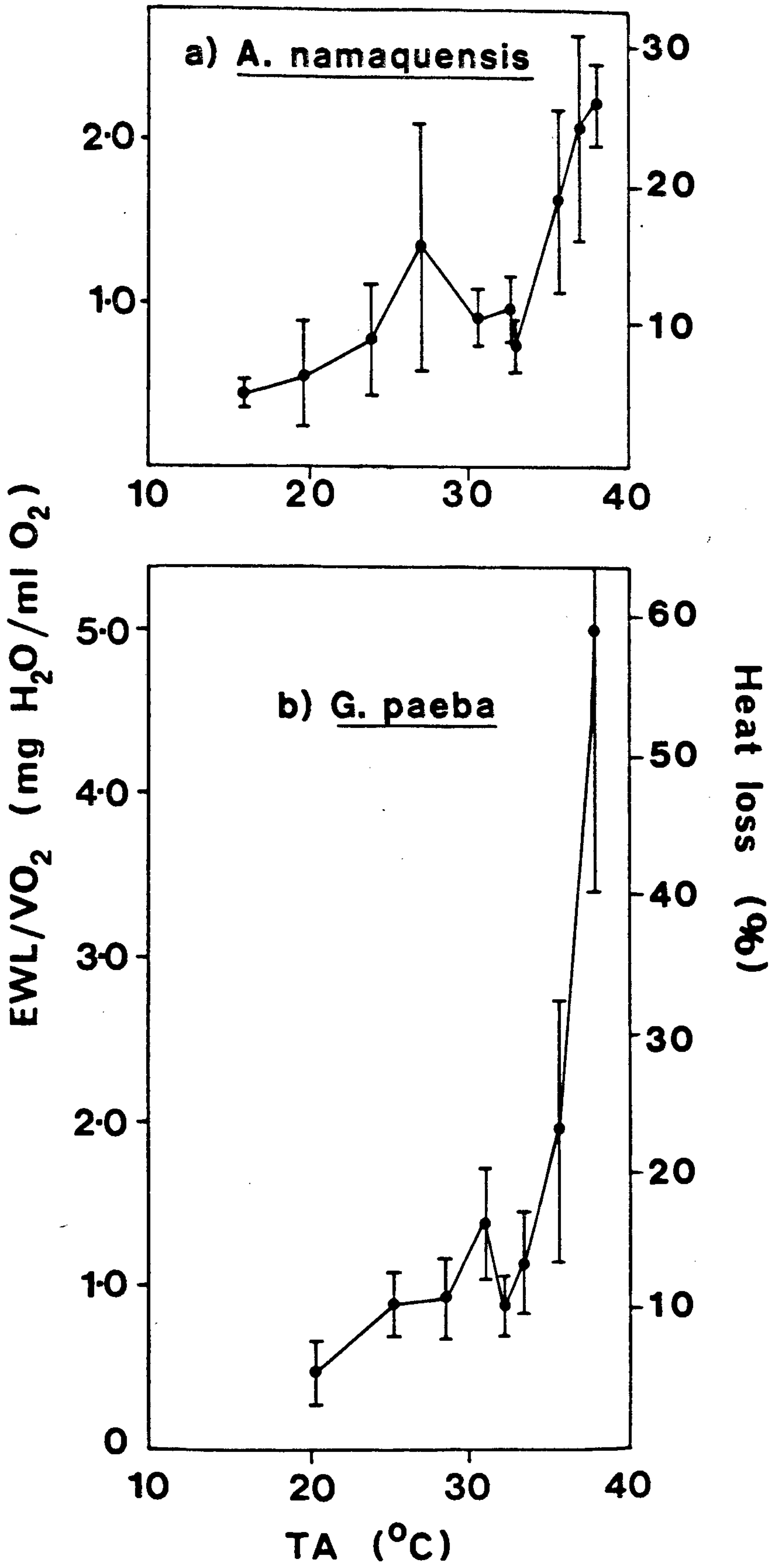
Minimal conductance values for both species were fairly constant below thermoneutrality. Mean minimal conductance for *G. paeba* between 20 - 30°C was significantly different to that in *A. namaquensis* ($p \leq 0.001$).

Minimal conductance values were also estimated from the slope of the equation relating oxygen consumption and ambient temperature below the region of thermoneutrality using McNab's (1980) correction factor:

$$Cm = Cf\ (0.06\ \copyright T + 1.00)$$

(where Cm is the minimal conductance ($cm^3O_2 . g^{-1}. °C^{-1}.h^{-1}$), Cf the fitted conductance from the slope of

Figure 4 : The effect of ambient temperature (TA) on i) (left hand ordinate) the ratios of evaporative water loss (EWL) to simultaneous oxygen consumption (VO_2) and ii) (right hand ordinate) evaporative heat loss as a percentage of metabolic heat production (HP) in a) *Aethomys namaquensis* and in b) *Gerbillurus paeba*. Values of 2.34 $J.mg^{-1}H_2O$ and 20.1 $J.cm^{-3}O_2$ were used to convert EWL and VO_2 to thermal units.


a) A. namaquensis
2·0
1·0
30
20
10
10
20
30
40
EWL/VO$_2$ (mg H$_2$O/ml O$_2$)
b) G. paeba
5·0
4·0
3·0
2·0
1·0
0
60
50
40
30
20
10
Heat loss (%)
10
20
30
40
TA (°C)

the line and ©T is the overestimation of body temperature from the intercept on the abcissa). The minimal conductance value for *A. namaquensis* estimated this way (0.096) was similar to the mean minimal conductance value (0.098) calculated. There was however a larger discrepancy between that estimated (0.144) and that obtained (0.156) for *G. paeba*. This discrepancy may by explained by the more labile body temperatures found in this gerbil and their effect on the rates of conductance. McNab (1980) suggested that in rodents that do not precisely maintain body temperature, minimal conductance from the slope of the line relating oxygen consumption to ambient temperature will be an underestimate and less accurate than that obtained from individual measurements, and this proved to be true for *G. paeba*.

Dry conductance

Below thermoneutrality, at temperatures less than 30°C, dry conductance in both species was fairly constant but were significantly different ($p \leq 0.002$). Above 30°C thermal conductance increased in both species (Table 1, Fig. 5)

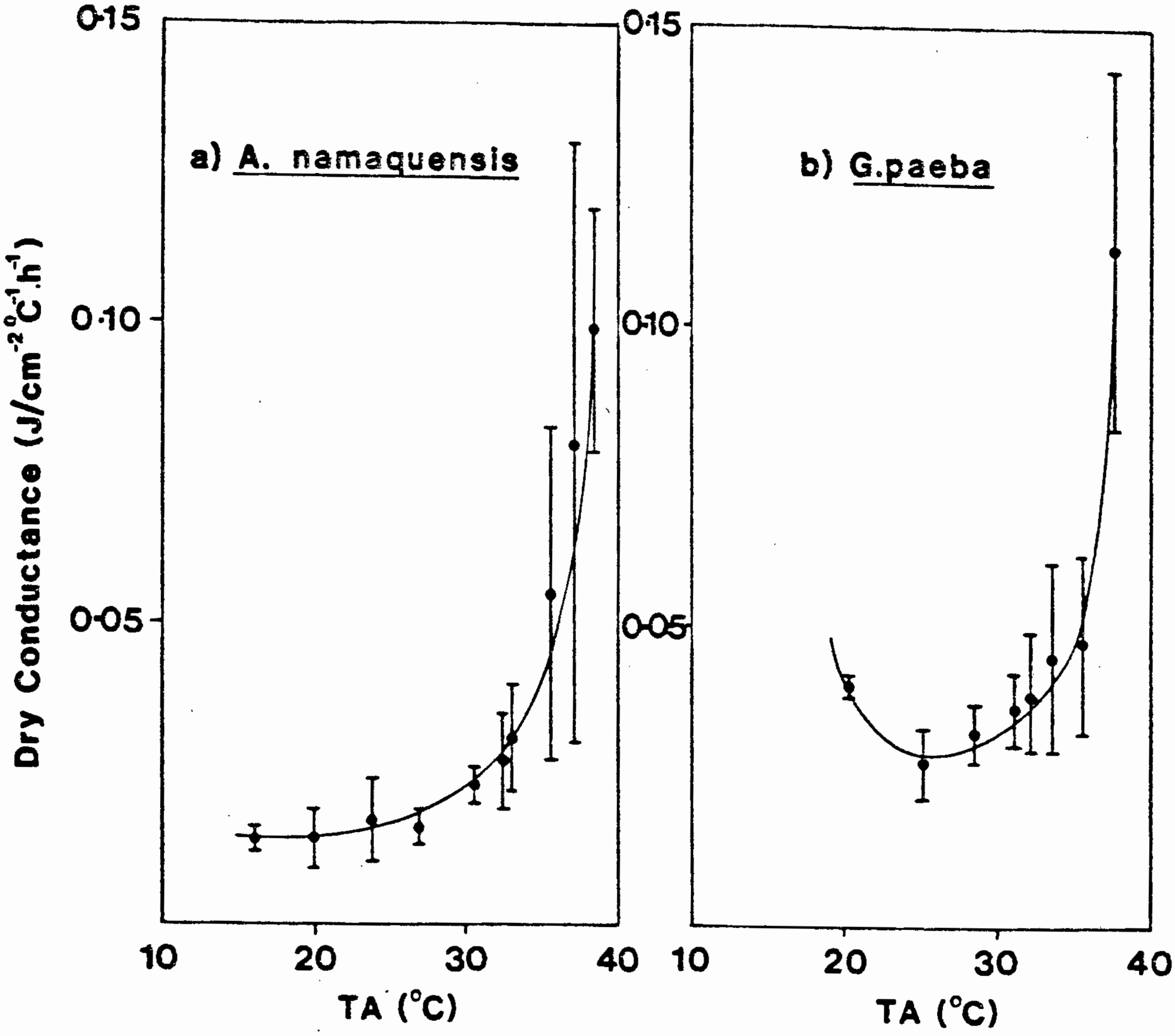


Figure 5 : Sensible thermal conductance of a) *Aethomys namaquensis* and b) *Gerbillurus paeba* at various ambient temperatures (TA)

Behavioural responses

During the resting phase, A. namaquensis was more easily disturbed than G. paeba. However, if not disturbed both species would remain inactive for long periods of time so facilitating measurements of resting rates. At low temperatures both species adopted spheripsoid postures and shivering was also observed.

Both species responded to increases in temperature beyond 30°C by altering their posture, so increasing their exposed surface area. As ambient temperature increased further, both species were observed to pant and salivate. Aethomys namaquensis licked most of its body until the fur appeared wet and matted, whereas G. paeba did not do this to the same extent but did exhibit more pronounced panting. Gerbillurus paeba became very restless at high ambient temperatures and spent long periods in frantic activity trying to escape from the chamber. These rodents succumbed rapidly (within 1.5 hours) to ambient temperatures of 38°C. Aethomys namaquensis, on the other hand, appeared to be more tolerant of increased ambient temperatures. It was less restless, lying prostrate for long periods and no fatalities occurred over the same temperature range, despite the fact that these rodents remained in the chamber for considerably longer periods (four hours).

DISCUSSION

Gaseous exchange

Both A. namaquensis and G. paeba conformed to trends found in most arid-adapted rodents (Hart, 1971; Borut and Shkolnik, 1974; McNab, 1979b) in that their basal metabolic rate was to be found lower than that predicted by Kleiber's (1975) allometric equation. The percentage deviation from that predicted was not significantly different in the two species, suggesting that lowered basal metabolic rate is an adaptation to reduced food supply and reduced respiratory evaporative losses as has been suggested by Bradley et al. (1974), rather than a response to limited gaseous and heat exchange in the confines of a closed burrow sustem as suggested by McNab (1966).

Reductions in gaseous exchange and the concomitant reduced chance of overheating and thermal death are no doubt a coincidental benefit for G. paeba and other burrow dwellers. Both species have a narrow thermoneutral zone of approximately 2.5°C. Reduced thermoneutral zones are a common phenomenon in small birds and mammals (Table 2) where large surface area / volume ratios and continually changing rates of conductance at temperatures close to this zone, affect

TABLE 2 Energy metabolism and thermoregulation in some nocturnal and semifossorial rodents and some truly fossorial rodents

	W	BMR***		C_m++		TB	TNZ	TA_L	F	Source
	(g)	$\bar{x}$	%*	$\bar{x}$	%**	°C	°C	°C	Ratio+	
CRICETIDAE										
Gerbillurus paeba	31	0.89	61	0.16	93	36	33 - 36	38	0.66	Present investigation
Gerbillus pusillus	13	1.05	58	0.24	89	35	32 - 38	41	0.65	Buffenstein & Jarvis (in press)
Meriones hurrianae	70	0.79	67	0.11	98	38	30 - 35	40	0.68	Goyal *et al.* (1982) & Ghosh (1975)
Meriones unguiculatus	67	1.60	134	0.80	263	38	-	40	0.51	Weiner & Gorecki (1981)
Neotoma lepida	110	0.79	75	0.07	79	37	25 - 33	38	0.95	Lee (1963)
Peromyscus eremicus	20	1.32	82	0.19	88	36	30 - 35	>39	0.93	McNab & Morrison (1963)
MURIDAE										
Acomys cahirinus	42	1.10	82	0.14	96	37	27 -> 33	40	0.86	Haim & Borut (1981)
Aethomys namaquensis	48	0.89	68	0.10	73	36	32 - 34	>38	0.93	Present Investigation
Leggadina hermannsburgensis	12	1.91	104	0.30	108	38	31 - 36	>37	0.97	MacMillen *et al.* (1972)
Notomys alexis	32	1.40	98	0.19	115	-	32 - 34	-	0.85	MacMillen & Lee (1970)
Notomys cervinus	34	1.22	86	0.19	113	38	33 - 33	-	0.76	MacMillen & Lee (1970)
TRULY FOSSORIAL										
Cannomys badius	344	0.50	63	0.05	102	36	27 -	-	0.62	McNab (1979a)
Geomys bursarius	197	0.70	77	0.12	184	35	30 - 33	-	0.42	Bradley & Yousef (1975)
Heterocephalus glauber	39	0.66	48	0.39	254	32	31 - 36	-	0.19	McNab (1966)
Microtus brandti	40	1.91	140	0.17	115	-	-	-	1.22	Weiner & Gorecki (1981)
Pitymys pinetorus	25	1.98	129	0.19	100	38	-	-	1.30	Bradley (1976)
Spalax leucodon	178	0.63	67	0.08	114	36	24 -		0.60	Gorecki & Christov (1969)
Tachyoryctes splendens	234	0.79	90	0.07	121	36	27 - 33	-	0.74	Packard (1968)
Thomomys talpoides	106	1.03	97	0.10	109	36	25 - 30	-	0.89	Bradley *et al.* (1974)
Thomomys umbrinus	85	0.85	75	0.12	119	35	27 - 35	-	0.63	Bradley *et al.* (1974)

*** $(cm^3\ O_2.g^{-1}.h^{-1})$

** $C_m(\%) = 100.Cm/(1.02.W^{-0.519})$, Aschoff (1981)

* $M_B(\%) = 100.BMR/(3.42.W^{-0.25})$, Kleiber (1975)

++ $(cm^3\ O_2.g^{-1}.°C^{-1}.h^{-1})$

+ $F = M_B(\%)/Cm(\%)$, McNab (1979)

the amount and rate of heat lost.

Evaporative water losses below the thermoneutral zone were similar ($p \geq 0.10$). Both species responded to the severe aridity of their environment by employing water conserving behavioural (posture) and morphological (see Schmidt-Nielsen *et al.*, 1970) mechanisms to ensure that pulmocutaneous evaporative water loss was minimal and essentially independent of ambient temperature. Evaporative water loss values expressed as a function of oxygen consumption were mid-range of those recorded of other nocturnal rodents in their thermoneutral zones (Table 2).

Body temperature

Recorded body temperature for *A. namaquensis*, over the experimental ambient temperatures of 10-33°C, fell within the range expected for typical eutherian mammals (Schmidt-Nielsen, 1975). This thermostability shown by *A. namaquensis* implies that it has a thermoregulatory capacity adequate to meet changes in ambient temperature. Even when resting, in its natural milieu, it is exposed to large diel temperature variations (±12°C pers. obs. and Withers, 1979) and it is therefore advantageous to maintain its independence of ambient temperature.

Gerbillurus paeba on the other hand, lives in a fairly deep burrow where ambient temperature is relatively constant (30 ± 1.0°C pers. obs.). In this study it did not show precise thermoregulatory control. At ambient temperatures less than 24°C, body temperature was directly proportional to ambient temperature. Nel and Rautenbach (1977) reported similar temperature variability for this species.

Differences in thermoregulatory control may be explained by the large differences in conductance between the two species ($p \leq 0.001$).

Conductance

Conductance is an indicator of the ease with which heat is transferred to or from the body. Minimal conductance below thermoneutrality was relatively constant in both species. This phenomenon is commom in rodents where large surface area / volume ratios preclude the maintenance of endothermy using physical thermoregulation alone and these small mammals are forced to rely on supplementary chemical thermoregulation, as reflected by linear increases in oxygen consumption (Bradley and Deavers, 1980).

Minimal conductance in *G. paeba* deviated by 7.27% from the predicted rate (Aschoff, 1981). This small difference indicates that it is as efficient as expected in its employment of physical thermoregulation and so conforms to the trends of conductance rates in most burrow dwellers. High minimal conductance is advantageous in the burrow context, for it limits heat storage. This reduces the chances of thermal death in an atmosphere characterized by high humidities which precludes the use of evaporative cooling. Minimal conductance values for *A. namaquensis* were significantly lower than those of *G. paeba* and deviated markedly (-26.8%) from that expected from Aschoff's (1981) allometric equation. This suggests that its powers of insulation are better than expected. This would be highly advantageous for a rodent living in a rock crevice where temperature fluctuations are greater than those in a plugged burrow. A low minimal conductance under these circumstances is adaptive in that it reduces the rate of heat loss (and hence additional energy requirements for chemical thermoregulation) at low ambient temperatures whilst also limiting the rate of physical heat gain at temperatures within the thermoneutral zone.

The ratio of the percentage expected metabolism and the percentage expected minimal conductance is a measure of the temperature differential between a homeotherm and the environment at the lower limit of thermoneutrality. This ratio may be used as an indicator of the ability to maintain homeothermy (Bradley and Yousef, 1975). A ratio of approximately one, as shown by *A. namaquensis* (0.96), is indicative of well developed endothermy. This confirms that *A. namaquensis* has balanced its low basal metabolic rate with high insulative properties (low conductance) to meet the demands of an environment, characterized by fairly large temperature ranges and not completely insulated from the effects of convection and radiation.

Gerbillurus paeba did not precisely maintain homeothermy. Considering that *G. paeba* is nocturnal, this labile body temperature seems strange, for the animal would have to contend with low ambient temperatures at night. Perhaps exercise at night is important in maintaining an elevated body temperature. In the confines of the thermally stable milieu *G. paeba* normally encounters when resting however, high minimal conductance and low basal metabolic rates in conjunction with the high burrow temperatures are adequate in maintaining endothermy. This degree of homeothermy as indicated by an F ratio of 0.67, whilst enough for its needs in the warm burrow context, is however, insufficient for maintaining body temperature at low ambient temperatures. Non-precise temperature regulation, when considered in conjunction with a basal metabolic rate 57% of the predicted minimum required for maintenance of endothermy (McNab, 1983), suggests that G. paeba employs torpor.

Response to high ambient temperatures

Aethomys namaquensis was less sensitive to temperature fluctuations than G. paeba. This finding is suggested by the fact that no deaths occurred in A. namaquensis at the highest temperatures monitored whereas three gerbils died within 1.5 hours of exposure to this ambient temperature. At ambient temperatures between the thermoneutral zone and 38°C, body temperature increased with increasing ambient temperature in both species. This hyperthermia, when converted to absolute quantities of heat stored using the specific heat capacity of mammalian tissue of $3.5 J.g^{-1}.{}^{\circ}C^{-1}$ (Mount, 1979), would save 0.264 mls H_2O. in A. namaquensis and 0.139 mls $H_2O.h^{-1}$ in G. paeba at an ambient temperature of 37.5°C. Aethomys namaquensis weighs 1.5 times as much as G. paeba. Proportionately greater tolerance to hyperthermia is therefore expected in view of its larger 'heat sink'. Aethomys namaquensis however stores more than 1.5 times as much heat, confirming that it is in fact more tolerant of hyperthermia than G. paeba.

Despite tolerance to hyperthermia, however, both species resorted to short term emergency evaporative cooling and increased conductance as a physiological defense mechanism against extreme heat. Small body size precludes the use of evaporative cooling alone as a homeostatic mechanism because of the relationship between surface area, heat load and transpiration (Mares *et al.*, 1977). *Aethomys namaquensis* was more parsimonious in evaporative water loss ($p \leq 0.001$) than *G. paeba*, dissipating 64% of that used by *G. paeba* in cooling at the highest temperatures monitored. Both *G. paeba* and *A. namaquensis* substantially increased evaporative water loss by salivation and panting. Panting, as reflected by the substantial increase in respiratory frequency, was more pronounced in *G. paeba*. In the confines of a plugged burrow, however, the high rates of evaporative water loss shown in the laboratory may be markedly reduced as evaporative water loss is impeded by high ambient humidities.

Above thermoneutrality, rate of heat loss was enhanced by increased conductance. This was facilitated by physiological (vasodilation) and morphological and behavioural means such as posture and activity. At high temperatures, *A. namaquensis* was observed grooming its fur so as to mat it. By incorporating all the above mentioned means, this species was able to increase its dry conductance to three times the thermoneutral zone value and so overcome the morphological and physiological properties it possesses for normally maintaining low rates conductance.

CONCLUSION

Despite the fact that *A. namaquensis* is a recent invader (Meester, 1965) of the extremely arid Namib desert, both this species and *G. paeba* (a long-term resident) appear to be well adapted, in that both species can survive indefinitely in diets of air dried seed (Buffenstein, in prep; Withers *et al*., 1980). Low basal metabolic rates in both species are adaptive features to the energetic limitations imposed by this harsh environment.

If coenothermy is to be maintained, rates of conductance must be modified so as to meet the demands of the milieu and compensate for reduced basal metabolic rates. The microclimate in a rocky crevice is not as stable or insulated from enviromental changes as that in a closed burrow. The crevice-dwelling rockrat, therefore requires better insulation than the pigmy gerbil, confined to its closed burrow. This gerbil depends on high rate of conductance to remove the superfluous heat produced in an enviroment where high ambient humidities preclude the efficient use of evaporative cooling.

When abnormally high ambient temperatures cannot be avoided, both species resort to emergency means of heat dissipation. These include forced evaporation cooling by salivation and panting and increased rates of conductance. *Gerbillurus paeba* was less tolerant of high ambient temperatures and succumbed at an ambient temperature of 38°C despite the fact that this species exhibited significantly higher rates of evaporative cooling. *Aethomys namaquensis* by tolerating a higher degree of hyperthermia was still able to show parsimonious water expenditures. Greater tolerance to high ambient temperatures is interpreted as a physiological adaption related to conditions encountered frequently in its milieu during the day.

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PART 4

CHAPTER 6

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

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Running title:
Physiological effect of high fibre diets.

Summary

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

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 diet with *ad lib.* water, DEE was 35% higher than the expected value. This discrepancy 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.

Water balance was assessed by measuring water lost and gained. Faecal water content was similar in both species, however urine concentrations and evaporative

water losses were higher in _G. paeba_. Observed differences in water loss are largely a function of parameters 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.

When provided with a more fibrous diet, low assimilation efficiency and the resulting increase in faecal production and concomitant faecal water loss precluded the maintenance of a positive water balance in either species. Despite increased urine concentration and reduced evaporative water loss, both species rapidly succumbed to chronic water deprivation.

Introduction

Since the early work of Schmidt-Nielsen et al. (1948) considerable information has accumulated on water balance and energy balance in arid-adapted rodents (see Schmidt-Nielsen, 1964; Chew, 1965; MacMillen and Hinds, 1983 for reviews). Nutritional requirements and daily energy expenditure (DEE) are also of interest to both the ecologist and the physiologist. These reflect not only the food resource demands but also the metabolic processes involved.

Ecological energetic parameters can be approached using a variety of techniques (see Gessaman, 1973; Grodzinski et al., 1975; Cloudsley-Thompson, 1976 for reviews). Most studies have examined the energetic requirements of small mammals by monitoring resting, standard or basal metabolic rates (McNab, 1970; 1979; Gessaman, 1973; Swan, 1974). Odum et al. (1962) and Drozdz (1968) suggest that monitoring food consumption over a longer period is more realistic, yet few recent studies (eg. McManus, 1974; Batzli and Cole, 1979) employ this technique. This indirect appraisal of energy requirements enables the monitoring of changes in energy intake and expenditure, whilst also allowing one to determine whether the food available has been used maximally. In addition, the potential significance of diet and apparent assimilation efficiency on the energy and water balance parameters may be assessed.

The Namib desert is an extremely arid environment in that the annual evapo-transpiration greatly exceeds the mean annual precipitation. The high rate of evapo-transpiration has a profound effect on the quality and sources of food available to its 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. Apart from the preformed water content, however, the importance of diet and digestive ability has been generally overlooked.

The rock rat, *Aethomys namaquensis*, and the pigmy gerbil, *Gerbillurus paeba*, whilst occupying different niches in the Namib desert are subject to similar energetic and water constraints. This study compares the changes in energy and water balance of these two Namib species when supplied with millet and deprived of water. In addition, this study addresses the problem of the effect of a high fibre food source on these parameters.

Methods

Fifteen gerbils and twelve rock rats were housed individually in an air-conditioned laboratory (20 ± 2 °C, 52,3 ± 9% relative humidity) with a twelve hour photoperiod. Prior to experimental treatments, rodents were maintained in plastic hamster cages with a sand substrate. This was removed during experimental runs, so as to prevent the contamination of food and faeces.

Over a six month period, all rodents were subjected to two experimental diets:- namely golden millet and Kelloggs 'high bulk bran' (see Table 1 for nutrient contents). A six week transition period occurred between these two food treatments, during which an *ad lib.* mixed bird seed supply (sunflower seeds, millet, oats, barley and bran) and *ad lib.* supply of fresh vegetables were provided. During this period the proportion of high bulk bran was gradually increased. Eventually, a pure bran diet was supplied for one week. 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. Four *G. paeba* and one *A. namaquensis* died from bloat when fed lucerne under *ad lib.* water conditions. Bran itself was fairly stressful even under *ad lib.* water conditions, in that,

TABLE 1 Food values of the two diets supplied to the animals

	Millet	High-Bulk Bran
Energy ($kJ.g^{-1}$)*	20.88	18.15
Protein (%)	12.70	18.00
Carbohydrate (%)	80.00	72.00
Fat (%)	3.50	1.40
Crude Fibre (%)	0.40	6.00
Dietary Fibre (%)	1.00	30.00
Preformed Water (%)	9.00	5.00

* Energy content was determined in this study. All other millet values were taken from Ockerman (1978). High-bulk bran data were supplied from the cereal manufacturers, Kelloggs (Braamfontein).

most rodents lost weight.

For the first two weeks of each food treatment, free water was supplied. During this period, the quantity of water drunk was monitored. Water bottles were then removed and exogenous water was supplied in the form of lettuce. This supply was gradually diminished over an eight day period. Thereafter no exogenous water was supplied and after five days, weight (to the nearest 0.01g), daily energy intake (DEI) and associated parameters were monitored. Water deprivation experiments were terminated when two animals per species had succumbed to hydropenia (deprivation of water).

Daily energy intake (DEI)

The DEI was determined gravimetrically from food consumption and faecal production. Food consumption was determined by initially supplying a known quantity of food greatly in excess of the gerbils' requirements. Unconsumed food was collected and weighed after six and twelve days. Control samples of the food were monitored for any weight changes and these were then corrected for in the results. 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. Daily energy intake was calculated from these values, according to the equation below:

$$DEI = GEI - TFE$$

where DEI is the daily energy intake ($kJ.g^{-1}.d^{-1}$), GEI is the gross energy intake ((mass of food eaten x energy provided by 1g food) /g body weight/day)in $kJ.g^{-1}.d^{-1}$. and TFE is total faecal energy ((mass of faeces x energy content of 1g of faeces)/g body weight/day) in $kJ.g^{-1}.d^{-1}$).

'Apparent' assimilation efficiency (AE) was calculated using the equation below:

$$AE = (DEI / GEI) \times 100$$

Urine energy content was ignored in these calculations. It has been found to constitute a negligble fraction of energy exchange (see Grodzinski and Wunder, 1975).

Metabolisable energy expenditure.

Experimental conditions were such that production was assumed to be zero, for only non-breeding adult gerbils were used. Daily energy expenditure was determined by including energy changes for the mobilization and deposition of fat (23.36 $kJ.g^{-1}$ fat mobilised and 33.9

$kJ.g^{-1}$ of fat deposited; Jagosz et al., 1979). It was assumed (as in Jagosz et al. (1979) and Withers (1982)) that mass changes were a result of fat utilization only and that changes in body water content were negligible. Daily energy expenditure was therefore assumed to represent only respiration required for body maintenance and activity.

Water Monitoring

All acclimated 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.

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 seeds was determined by drying known quantities of seed at 60°C to constant mass. Metabolic water was calculated assuming 0.03ml $water.kJ^{-1}$ (Schmidt-Nielsen, 1975).

Faecal water loss was determined by measuring the faecal water content in faeces voided, whilst handling the rodents. Faeces were stored individually in small weighed microvials and these were reweighed as soon as possible on an electronic microbalance to the nearest 0.01mg. Faeces in the microvials were then dried at 60 °C to constant mass and reweighed.

Water loss in the urine was determined by collecting 24-hour urine samples under light liquid paraffin. The total volume of the urine excreted was measured by weighing the urine sample and a 10µl aliquot, so that by correcting for density mass could be converted into volume.

Urine concentrating capacity was examined by monitoring changes in osmolality (using a vapour pressure osmometer). These urine concentrations were then compared to those of blood. Blood was taken from the canthal sinus on the anteriodorsal aspect of the orbit, according to the method of Halpern and Pacaud (1951). Blood samples of 200µl were collected in heparinised capillary tubes and centrifuged. Haematocrit measurements were taken, thereafter plasma was separated and frozen in sealed capillary tubes for analysis.

Dietary water index (IDW) for quantifying the water gain or loss from ingested food was calculated according to Bartholomew's (1975) equation:-

$$\text{IDW} = \frac{\text{preformed water in food}}{\text{water in excreta}}$$

This formula is based on the assumption that evaporative water loss is approximately equal to metabolic water liberated during the oxidation of hydrogen in the food. If IDW = 1, water is neither lost nor gained as a result of eating. If IDW is less than 1, eating increases the rate of water loss and if IDW is greater than 1, eating results in a net gain of water.

Statistical analyses included student-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. Three G. paeba died within seven days of water-deprivation and two A. namaquensis died the following day. The severity of the bran diet when hydropenic is indicated by the rapid weight loss shown by both species (Fig. 1).

Gut morphology

Kostelecka-Myrcha and Myrcha (1964) suggested that the relative length of the hind gut (caecum and large intestine) in rodents is indicative of the diet eaten and more specifically of the normal proportion of plant material in the diet. Gross gut morphology values for A. namaquensis and G. paeba are given in Table 2.

The ratio of the length of the large intestine and caecum to the total intestinal tract was 1.5 times greater in A. namaquensis, suggesting that more caecal fermentation occurs in this species. Differences in the hind gut ratios also suggest that there is a tendency towards greater adaptation to herbivory

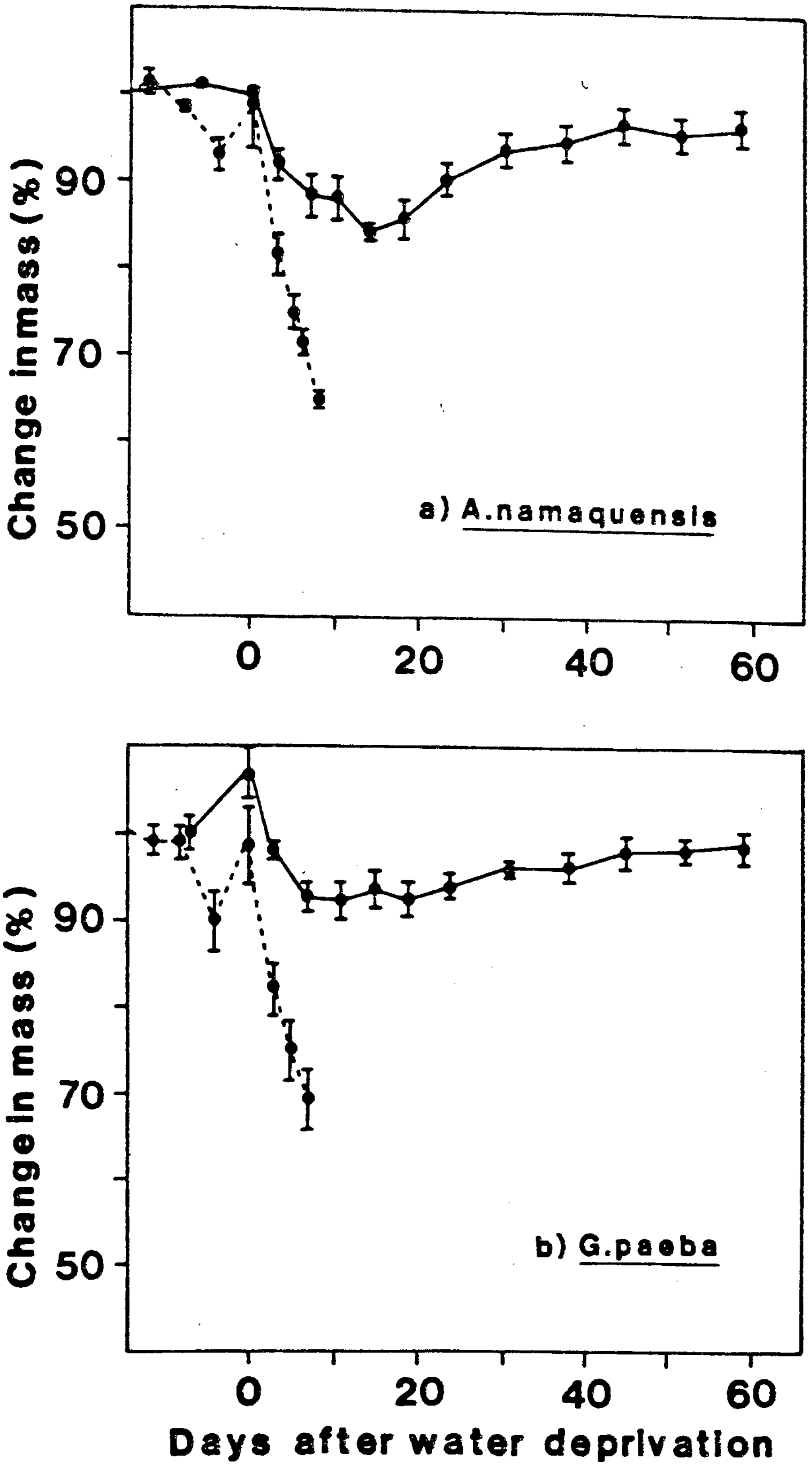

Figure 1 : Changes in mass for a) *Aethomys namaquensis* and b) *Gerbillurus paeba* when deprived of water on i) a low fibre diet of millet and ii) a high fibre diet of bran. Values are means and standard errors.

TABLE 2 Gastro-intestinal measurements expressed as a percentage of total length

		A. namaquensis	*G. paeba*
(a)	Stomach	9.7 ± 0.9	6.0 ± 0.2
(b)	Small intestine	50.6 ± 2.4	67.1 ± 0.7
(c)	Caecum	13.3 ± 0.5	5.8 ± 0.2
(d)	Large intestine	26.4 ± 0.9	21.3 ± 1.1
(e)	Hind gut ((c) & (d))	39.7 ± 1.2	27.0 ± 0.9

(Morton, 1979; Perrin and Curtis, 1980) in *A. namaquensis*.

Daily energy expenditure

Both species under *ad lib.* water conditions showed similar changes in mass and digestive ability ($p \geq 0.10$). Rates of consumption, faecal production and GEI (Tables 3 & 4) were however significantly different ($p \leq 0.05$). The slight differences in these mean values when combined become more pronounced and both DEI and DEE were highly significantly different ($p \leq 0.001$). This difference in DEE does not merely reflect differences in mean body mass, for percentage deviations were significantly different from those predicted by mass for a granivorous rodent using Grodzinski and Wunder's (1975) allometric equation.

Despite the fact that bran was gradually introduced into the diet, this food was generally avoided. The 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 4), reflecting the high fibre content of this food supply, and no species difference was observed.

Energetic responses to water deprivation

Millet

Gerbillurus paeba and *A. namaquensis* showed different initial responses to water deprivation when maintained on a millet diet. *Gerbillurus paeba* showed an initial increase in DEE during the first week of water deprivation, although once body mass had stabilized DEE rates returned to within the range observed under *ad lib.* conditions (Table 3).

Aethomys namaquensis lost weight more gradually but continued to do so for much longer (Fig. 1). No significant changes were observed in any of the energetic balance parameters monitored on the millet diet (Table 3) in this species.

Bran

On a bran diet, DEI declined significantly with water deprivation in both species (Table 4). When on an *ad lib.* diet, the apparent assimilation efficiency was not significantly different to that with water deprivation, as a proportionate decline in faecal production accompanied the reduced intake. *Aethomys namaquensis* supplemented its reduced DEI with energy from the mobilization of fat reserves and so maintained its DEE.

TABLE 3 Changes in energy balance in *Aethomys namaquensis* and *Gerbillurus paeba* with hydropenia when maintained on a low fibre diet (millet)

	+ H_2O		− H_2O 1 week		− H_2O 2 weeks	
	$\bar{x}$	$\pm$ S.D.	$\bar{x}$	$\pm$ S.D.	$\bar{x}$	$\pm$ S.D.
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* (kJ.g^{-1}.day^{-1})	1.64	0.16	1.45	0.22	1.54	0.21
FE* (kJ.g^{-1}.day^{-1})	0.93	0.03	0.09	0.04	0.08	0.04
ME* (kJ.g^{-1}.day^{-1})	-0.08	0.08	0.18	0.17	-0.08	0.28
DEI* (kJ.g^{-1}.day^{-1})	1.55	0.15	1.36	0.20	1.45	0.20
DEE* (kJ.g^{-1}.day^{-1})	1.46	0.13	1.55	0.12	1.53	0.17
AE (%)	94.31	1.95	93.98	2.43	94.60	2.27
DEE* (%)	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* (kJ.g^{-1}.day^{-1})	2.60	0.30	2.41	0.39	2.71	0.33
FE* (kJ.g^{-1}.day^{-1})	0.12	0.04	0.09	0.03	0.10	0.03
ME* (kJ.g^{-1}.day^{-1})	-0.04	0.29	0.42	0.28	-0.13	0.16
DEI* (kJ.g^{-1}.day^{-1})	2.48	0.26	2.32	0.40	2.60	0.31
DEE* (kJ.g^{-1}.day^{-1})	2.48	0.27	2.74	0.29	2.50	0.31
AE (%)	95.53	1.12	96.15	1.34	96.21	0.72
DEE* (%)	134.92	7.92	145.46	9.20	130.97	15.76

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

TABLE 4 Changes in energy balance in *Aethomys namaquensis* and *Gerbillurus paeba* on a high fibre diet (bran)

	Aethomys namaquensis				*Gerbillurus paeba*			
	+ H_2O		- H_2O		+ H_2O		- H_2O	
	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.
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 ($kJ.g^{-1}.day^{-1}$)	1.64	0.32	0.62	0.12	2.78	0.88	0.67	0.27
FE ($kJ.g^{-1}.day^{-1}$)	0.60	0.17	0.20	0.04	0.99	0.33	0.24	0.11
ME ($kJ.g^{-1}.day^{-1}$)	0.29	0.17	1.11	0.18	0.04	0.27	0.60	0.17
DEI ($kJ.g^{-1}.day^{-1}$)	1.04	0.25	0.42	0.11	1.79	0.56	0.39	0.11
DEE ($kJ.g^{-1}.day^{-1}$)	1.33	0.19	1.52	0.25	1.83	0.40	1.03	0.12
AE (%)	63.31	8.69	66.82	6.10	64.45	2.10	64.58	7.02
DEE (%)*	101.99	13.40	98.76	21.89	97.99	22.08	46.85	6.66

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

In G. paeba, DEE expressed as a percentage of body mass declined to approximately half of that observed when deprived of water on a millet diet

Water Balance

Water intake

Drinking rates of the two species were not significantly different ($P \geq 0.1$). Both species drank significantly more water (Tables 5 & 6) on the bran diet than when millet was the food source ($p \leq 0.001$). Species differences in total water intake reflect mainly differences in the amount of water liberated from their different rates of metabolism (Tables 5 & 6).

Water losses were significantly different. Urine production when drinking water was freely available was significantly greater ($p \leq 0.01$) in G. paeba, reflecting the greater volumes drunk by this species (Tables 5 & 6).

Under conditions of water deprivation, urine production of both species declined markedly on both diets. However this change with hydropenia was most pronounced

TABLE 5 Changes in water balance in *Aethomys namaquensis* and *Gerbillurus paeba* with hydropenia when maintained on a low fibre diet (millet)

	Aethomys namaquensis						*Gerbillurus paeba*					
	+ H_2O		- H_2O 1. week		- H_2O 2 weeks		+ H_2O		- H_2O 1 week		- H_2O 2 weeks	
	$\bar{x}$	$\pm$ S.D.	$\bar{x}$	$\pm$ S.D.	$\bar{x}$	$\pm$ S.D.	$\bar{x}$	$\pm$ S.D.	$\bar{x}$	$\pm$ S.D.	$\bar{x}$	$\pm$ S.D.
Intake :												
Drunk (mg $H_2O.g^{-1}.day^{-1}$)	95.2	30.4	-	-	-	-	117.1	47.7	-	-	-	-
Preformed water (mg $H_2O.g^{-1}.day^{-1}$)	7.1	0.7	6.3	0.9	6.6	0.9	11.2	1.3	10.0	1.7	11.7	1.4
Metabolic water (mg $H_2O.g^{-1}.day^{-1}$)	43.8	3.9	46.5	3.6	45.9	5.2	74.4	8.5	82.2	8.8	74.9	9.2
Total intake (mg $H_2O.g^{-1}.day^{-1}$)	146.1	29.2	52.8	4.1	52.7	5.1	202.6	48.6	92.6	10.2	86.5	10.5
Loss :												
Urine (mg $H_2O.g^{-1}.day^{-1}$)	20.9	6.0	8.3	4.1	8.1	3.2	40.8	18.1	5.8	2.3	4.4	2.8
Faeces (mg $H_2O.g^{-1}.day^{-1}$)	5.4	1.9	3.8	1.9	3.7	1.7	7.5	2.4	3.8	1.1	4.7	1.1
EWL (mg $H_2O.g^{-1}.day^{-1}$)	119.8	26.1	40.7	7.2	40.7	4.9	15.5	33.7	83.1	8.7	77.5	11.0

TABLE 6 Changes in water balance in *Aethomys namaquensis* and *Gerbillurus paeba* with hydropenia when maintained on a high fibre diet (bran)

	Aethomys namaquensis				*Gerbillurus paeba*			
	+ H_2O		- H_2O		+ H_2O		- H_2O	
	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.
Intake :								
Drunk (mg $H_2O.g^{-1}.day^{-1}$)	215.5	72.7	-	-	283.9	58.3	-	-
Preformed water (mg $H_2O.g^{-1}.day^{-1}$)	4.6	0.9	1.8	0.3	7.8	2.6	1.9	0.6
Metabolic water (mg $H_2O.g^{-1}.day^{-1}$)	40.1	5.9	45.7	7.6	55.0	12.1	31.0	3.4
Total intake (mg $H_2O.g^{-1}.day^{-1}$)	248.5	61.0	47.5	7.9	342.5	60.4	32.9	3.4
Loss :								
Urine (mg $H_2O.g^{-1}.day^{-1}$)	56.9	5.6	8.5	4.3	109.6	37.3	4.6	2.9
Faeces (mg $H_2O.g^{-1}.day^{-1}$)	49.4	13.9	11.9	2.2	102.4	57.9	13.3	6.0
*EWL (mg $H_2O.g^{-1}.day^{-1}$)	137.7	63.9	27.0	6.3	130.2	33.7	15.0	7.9

when high-bulk bran was the food source (Table 6). Urine concentration was inversely proportional to the quantity of urine produced and was highest when the rodents were on a diet of bran (Table 7).

Both species irrespective of diet, produced faeces with similar water contents ($p \geq 0.1$). When deprived of water, faecal water content declined (Table 7). Faecal water content was greater on the bran diet than on the equivalent millet diet. Consequently, when maintained on a bran diet, faecal water loss contributed significantly more to the total water flux (Table 7).

Pulmocutaneous evaporative water losses as extrapolated from water balance parameters were similar for both diets when drinking water was freely available. When deprived of water while on a millet diet (Table 5), *A. namaquensis* exhibited lower pulmocutaneous evaporative losses than *G. paeba* ($p \leq 0.001$). When on a bran diet, however, *G. paeba* showed lower pulmocutaneous evaporative water losses than *A. namaquensis* (Table 6).

TABLE 7 Changes in plasma and urine osmolality and faecal water loss when *Aethomys namaquensis* and *Gerbillurus paeba* are deprived of water and maintained on a low fibre diet (millet) and a high fibre diet (bran). (Means $\pm$ S.D. are shown.)

	Plasma conc. (m Osm. l^{-})		Urine conc. (m Osm. l^{-})		Faecal water content (%)		Faecal water loss (%)	
	$\bar{x}$	$\pm$ S.D.	$\bar{x}$	$\pm$ S.D.	$\bar{x}$	$\pm$ S.D.	$\bar{x}$	$\pm$ S.D.
MILLET								
A. namaquensis								
+ H_2O	332	36	1762	914	53.08	2.98	3.97	2.04
- H_2O 1 week	-		3263	474	45.35	2.86	7.16	3.38
- H_2O 2 weeks	396	52	3732	610	45.70	2.96	6.97	2.69
G. paeba								
+ H_2O	350	37	2576	1178	54.01	3.31	3.79	1.31
- H_2O 1 week	-		3956	499	44.52	2.57	4.11	1.14
- H_2O 2 weeks	426	57	4150	1087	46.47	3.59	5.38	1.04
BRAN								
A. namaquensis								
+ H_2O	337	51	1710	197	58.05	0.71	21.39	8.95
- H_2O	414	64	4396	837	50.68	1.95	25.41	4.97
G. paeba								
+ H_2O	362	49	1679	313	60.97	1.47	28.81	12.32
- H_2O	471	68	5615	816	49.99	1.20	41.07	20.54

Discussion

Millet

Like most arid-dwelling rodents (Reichman, 1981), both G. paeba and A. namaquensis consume a fair proportion of seed in the natural diet (Table 8). 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 observed in this study under ad lib. water conditions was similar to those observed by Withers et al. (1980). However, DEE for G. paeba were much lower than those reported by Withers et al. (1980). Nevertheless, in both cases, DEE for G. paeba was far greater than that predicted by mass. Withers et al. (1980) suggested that high DEE values might merely reflect hyperactivity in the laboratory. The DEE values for G. paeba are more in line with that predicted allometrically (Grodzinski and Wunder (1975) for an insectivorous rodent (2.34 kJ. day^{-1}). The discrepancy between observed and predicted values might however indicate a greater propensity of G. paeba to supplement its seed diet with insects. This is confirmed by stomach content data (Table 8). Both species maximally utilized their food source, having high assimilation efficiencies. These were similar to those reported for other rodents (Johnson and Schreiber, 1979).

Both _A. namaquensis_ and _G. paeba_ showed similar physiological adaptations to their environment and responded well to hydropenia. Neither species succumbed to dehydrational stress on a millet diet and the experiment was terminated after 10 weeks without exogenous water. This ability to survive indefinitely without water is a common feature in arid-adapted rodents (Schmidt-Nielsen, 1964; Chew, 1965; Shkolnik and Borut, 1969; Bradley and Yousef, 1972; MacFarlane, 1975) and is mainly due to a decline in water expenditure through reduced evaporative water loss, reduced faecal water content and increased urine concentration, with the concomitant decline in urine volume.

Initial responses to hydropenia were different in the two species in that _G. paeba_ showed a greater weight loss (Fig. 1). This increased weight loss was reflected in the significant increase in DEE in the first week of water deprivation. Thereafter weight stabilized in this species and the DEE returned to predeprivational rates. This increase in DEE does not represent significant changes in food consumption or digestive ability, but can be attributed only to fat mobilization. This might reflect increased metabolic stress or hyperactivity resulting from increased searching for a water supply. Or it may also be merely a consequence of an erroneous assumption that all mass

TABLE 8 Stomach contents of kill-trapped rodents

		n	Seed		Insects		Leaf		Stem	
			$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S.D.
*Aethomys namaquensis**		16	32.3	35.2	21.3	37.6	19.1	21.2	27.2	32.0
*Gerbillurus paeba***	6/1976	6	55.6	29.4	5.2	3.7	27.0	28.2	9.8	15.9
	10/1976	11	36.6	30.6	49.0	31.0	9.5	18.2	1.8	5.2
	4/1977	7	24.2	8.5	69.4	9.2	2.8	2.0	0.1	0.4

Sources : * Withers, 1979

** Buffenstein, 1977

change is a result of fat mobilization rather than a result of dehydration. Aethomys namaquensis showed a more gradual weight loss, mass only stabilizing after 13 days of hydropenia. It continued to lose weight throughout the period when food consumption was monitored. This helped to maintain the DEE at approximately the same level as under ad lib. water conditions. Withers et al. (1980) reported a decline in the DEE with water deprivation. These anomalous findings might be due to the small sample (two) used by Withers et al. (1980). Their DEE values fall within the lower range of values measured in this study. The coefficient of digestive ability remained high with water deprivation. This high rate is advantageous, in that it not only enables maximum utilization of resources, but at the same time reduces the faecal output, thereby reducing the quantity of water lost through the faeces.

Weight-relative water requirements were found to be significantly different ($p \leq 0.05$). Gerbillurus paeba, having a higher DEE, liberated more metabolic water ($p \leq 0.001$). These direct measurements of 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 seemed initially more stressed with water deprivation. However after only six days without free water, mass stabilized as the animals adapted to water shortage and effective hormonal control had commenced. This initial stress at first seems incongruous as more metabolic water was liberated in this species. The water lost under laboratory conditions appeared to be mainly through evaporative water loss. Because G. paeba has a smaller body size than A. namaquensis its surface-area / volume ratio and weight specific metabolic rates are higher. These resulted in a higher rate of evaporative water loss and hence its 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 prep).

Gerbillurus paeba had an IDW of 1.3, suggesting that it derives some gain in water balance by eating seed and that increased metabolic water as a result of its higher DEE was sufficient to meet its high rate of evaporative water loss. Aethomys namaquensis had an IDW of 0.6, implying that it could not maintain a positive water balance and should therefore be unable to survive without additional water. This was not the case. *Aethomys namaquensis* lost weight for a longer period though it did so at a fairly gradual rate. Total metabolic water liberated exceeded water lost through pulmocutaneous evaporation. This saving in evaporative water loss was sufficient to ensure virtual independence of exogenous water.

Despite differences in water flux, namely greater urine concentration in *G. paeba* and a larger reduction in evaporative water loss in *A. namaquensis*, both species when hydropenic were able to maintain a positive water balance on millet. When this seed diet was replaced with a more fibrous diet, however, they were unable to do so.

Bran

The digestive ability coefficient on this diet was much lower than that when millet was the food source. Shenk *et al*. (1970) reported that digestive ability varied inversely with fibre content when semi-synthetic diets were fed to *Microtus pennsylvanicus*. Digestive ability on a bran diet was lower than recorded for rodents on a natural diet (Johnson and Schreiber, 1979) and a bran diet 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 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 to the intake 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. This 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.

When water deprived, GEI in both species was markedly reduced. If GEI had remained at *ad lib.* rates, faecal water loss would have forced both species into an immediate negative water balance. Even with this decline in food consumption, and therefore faecal production, faecal water loss during hydropenia was 3-4 times greater than that observed on the millet diet. *Aethomys namaquensis* maintained similar levels of DEE on both diets. This was achieved by balancing the energy intake deficit with energy stored as fat. In addition, although still much lower than on a millet diet, the apparent assimilation efficiency increased with hydropenia. This increase in assimilation efficiency is a common occurrence when food intake is reduced. Reduced food intake allowed for a slower rate of passage and hence the opportunity for more absorption. Possibly water reabsorption may be improved by the slower rate of passage.

It is not known whether *A. namaquensis* uses coprophagy. *Aethomys namaquensis* has been seen licking faeces in the laboratory though it has not been observed eating them. Under stressful conditions coprophagy would be advantageous.

Gerbillurus paeba, on the other hand, showed a marked decrease in DEE accompanied by a decline in evaporative water loss and also a decline in apparent assimilation efficiency. These findings suggest that *G. paeba* employs torpor under these circumstances. Similar declines in DEE, assimilation efficiency and evaporative water loss has been observed in *G. pusillus* when employing torpor (Buffenstein in press).

Neither species survived more than eight days without free water. The IDW for both species were approximately 0.1. This is one tenth the value determined by Bartholomew (1975) for maintaining water balance. The very low IDW implies that the more these animals ate, the more dehydrated they would become. The inability of either species to survive this treatment may be attributed to the low assimilation efficiency and the resulting increase in faecal production, precluding the maintenance of a positive water balance. Although *A. namaquensis* consumes proportionately more fibrous food than *G. paeba* in its natural diet and its gastro-intestinal tract is morphologically better adapted to handle fibrous food, through caecal fermentation, it too could not survive high fibre diets in which the preformed water was low.★

ADDENDUM

★ Whilst it is clearly evident that the high fibre content increased faecal water loss such that the rodents were forced into a negative water balance, the additional protein load (Table 1) may also have contributed to increased urine osmolality. It is unlikely, however, that protein loading would affect the quantity of urine voided.

Dipodomys, *Notomys* and *Jaculus* (Deavers and Hudson, 1979; Hewitt, 1981). These authors suggested that the stimulus of water deprivation increases renal efficiency to the maximum possible through the medullary area whilst also augmenting permeability-controlled solute recycling in the renal pelvis.

On a bran diet, pulmocutaneous evaporative water loss declined markedly with hydropenia. Whilst reduced evaporative water loss is a common occurrence with hydropenia, the very low values obtained might indicate that the assumption that a homeostatic state is maintained is erroneous. Pulmocutaneous evaporative water loss values obtained in this study suggest that water was mobilized from various compartments in the body and that these rodents had become dehydrated. This was substantiated further by elevated haematocrits and increased plasma osmolality in both species. Neither species was therefore able to eliminate sufficient quantities or electrolytes of urea and conserve sufficient water to prevent haemoconcentration. Similar haemoconcentration has been observed in other arid-dwelling rodents eg. Dipodomys (Kenagy, 1973; Skelza and Knoll, 1982), Gerbillus, Jaculus (Haggag and El Husseini, 1974), Rattus (Baverstock, 1976) and in Meriones (Donaldson and Edwards, 1981).

It is clearly evident that increased faecal water loss (Table 7), 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 that diet selection against high fibre foods in the wild would be critical during the periods when water is severely limiting. Stomach contents (Table 8) and observations in the laboratory have shown that _G. paeba_ avoids foods high in fibre when water stressed, supplementing its granivorous diet with the high water content insect tissue. The higher water content of this food source was adequate for the maintenance of a positive water balance and also enabled easy removal of the concomitant increased nitrogen load, so ensuring _G. paeba_'s survival. _Aethomys namaquensis_ did not appear to be as selective in its diet choice. Withers (1979) found this species had a high mortality rate, and a high reproduction rate. The high mortality rate might be attributed to the high fibre content of its less specialised diet and its inability to survive periods of water stress when the food source is high in fibre. This species must therefore compensate for its high mortality rate, by having a high reproductive rate in its natural milieu.

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PART 5

CHAPTER 7

Identification of crystalline allantoin in the urine of African Cricetidae (Rodentia) and its role in their water economy.

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Running title: Crystalline allantoin in cricetid urine.

Summary

All eleven cricetid species, examined in this investigation, produced an off-white crystalline precipitate in their urine when deprived of water, whereas not one murid did so. This crystalline compound was identified as allantoin, the common end product of purine metabolism. The quantity found in the solid precipitate alone accounted for 47% of the total nitrogen excreted and was approximately 14 times greater than the predicted quantity of allantoin from purine degradation. It appears that there is a shift in the biochemical pathway of nitrogenous excretion from urea to allantoin in the Cricetidae.

The cricetids had higher urine osmolalities (4854 ± 87mOsm.kg^{-1}) and urea concentrations (3227 + 122mM.l^{-1}) and lower daily percentage body water turnovers (1.58 ± 0.74) than the murids (3621 ± 79mOsm.kg^{-1}; 2239 ± 147mM.l^{-1}; 2.05 ± 0.76%.day^{-1} respectively). This can be explained by the substantial water savings associated with excreting solid allantoin. The discrepancy in the mode of nitrogen excretion between the two families inhabiting the Namib Desert can be attributed to their differing evolutionary histories, the Cricetidae being pre-adapted for survival in desert niches.

Introduction

Rodents are an important faunal element in arid environments. Much attention has been directed towards the physiological, morphological and behavioural attributes which favour their survival in these environments (Schmidt-Nielsen, 1964; MacMillen et al., 1972; Borut & Shkolnik, 1974; Ghobrial & Nour, 1975; Mares et al., 1977; Christian, 1979). Their physiological adaptations, however, might in part reflect their different evolutionary histories and their various taxonomic affinities.

During an investigation of the effect of water deprivation on arid-adapted rodents from the Namib desert, it was observed that when deprived of water, two cricetid species, Gerbillurus paeba and Gerbillurus tytonis, produced large quantities of off-white needle-like crystals whilst a third species, the murid Rhabdomys pumilio, did not (Buffenstein, 1977). Owing to the relative abundance of this substance in the urine of water-stressed Gerbillurus and the possibility that it might play an important role in its renal physiology, its investigation was undertaken. In addition, water economy and renal efficiency of several species of rodents from the arid regions of southern Africa were compared in an attempt to elucidate the physiological role of this substance.

Procedure

Animals

Rodents were live-trapped using Sherman traps baited with a mixture containing peanut butter, dried fruit and seed. The following murid and cricetid species, based on the classification of Missone (1974), were collected from the arid regions of the Cape Province (South Africa) and Namibia :- i) Muridae; *Acomys subspinosus*, *Aethomys chrysophilus*, *Aethomys namaquensis*, *Praomys natalensis*, *Rhabdomys pumilio* and *Thallomys paedulcus*; ii) Cricetidae; *Desmodillus auricularis*, *Gerbillurus paeba*, *Gerbillurus setzeri*, *Gerbillurus tytonis*, *Saccostomys campestris* and *Tatera leucogaster*. In addition, we collected two arid-adapted cricetid species from north-eastern Kenya, *Gerbillus pusillus* and *Tatera robusta*, and four cricetid and four murid species from mesic areas in the Cape Province, namely *Gerbillurus paeba*, *Malocothrix typica*, *Steatomys krebsii* and *Tatera afra* and *Acomys subspinosus*, *Aethomys namaquensis*, *Mus musculus* and *Rhabdomys pumilio*.

The rodents were housed individually and supplied *ad lib*. with golden millet and their exogenous water in the form of green vegetables. They were left to acclimate to their new environment (12hL: 12hD, 22-26°C, 45-60% humidity) for two months prior to deprivation of water (hydropenia).

Hydropenia

The exogenous supply of water was gradually decreased by reducing the daily ration of green vegetables to zero over eight days. Thereafter no free water was provided. Animals were weighed regularly on a Mettler balance to the nearest 0,01g. In non arid-adapted species, if weight loss exceeded 30% of the initial body mass, water in the form of green vegetables was again supplied.

Urine

Twenty-four hour urine samples were collected once the mass of all arid-adapted rodents had stabilised (six weeks after commencement of water deprivation) and after six days in non arid-adapted species. Urine samples were collected by housing each rodent in a small glass aquarium (300 x 230mm) which was placed upside down on a stainless steel mesh grid. Millet seed was supplied ad lib. for two hours at the beginning of the scotophase. A large rectangular container (400 x 280mm) containing light liquid paraffin was placed beneath the grid. Urine was collected under this mineral oil. It was pipetted out and stored in plastic vials (Eppendorf 1.5ml) and frozen (-15 °C) until analysis. As some contamination with faeces was inevitable, contaminated urine was stored separately. Care was taken to collect all the urine and its crystalline component.

Prior to the analysis of the urine, it was centrifuged for ten minutes and the liquid fraction decanted into Eppendorf vials of known mass. The total volume of urine excreted per day was determined by weighing the urine and a separate 10µl aliquot, thus converting mass into volume. If the urine had a crystalline component the crystalline component was dried at 28 °C and weighed before being filtered using a Buchner funnel, thoroughly washed with ethanol and left to dry.

Blood collection

Blood samples were taken, just prior to the resupplying of free water, from the canthal sinus of the anterio-dorsal aspect of the orbit, according to the method of Halpern & Pacaud (1951). Blood was collected in heparinised capillary tubes and centrifuged for five minutes. Haematocrit readings were taken before the plasma was separated from the packed cells and frozen until analysis.

Urine and plasma analysis

Osmolality was determined using a vapour pressure osmometer (Wescor model 5100B). The spectrophotometric method of Chaney and Marbach (1962) was used for measuring urea concentrations. Uric acid concentrations were determined by using the enzymatic colorimetric assay of Kageyama (1971). Allantoin concentrations dissolved in the urine were monitored according to the methods of Young & Conway (1942) and Vrbaski *et al*. (1978).

Chemical analysis of the crystalline precipitate

The crystalline precipitate from the urine of *D. auricularis*, *G. paeba* and *T. leucogaster* was examined thoroughly using 1H-nuclear magnetic resonance (1H-nmr), infra red (IR) and mass spectrometry. The IR spectra were run as Nujol mulls. The 1H-nmr spectra were recorded in hexadeuterodimethyl sulfoxide at 100Mhz, using tetramethylsilane as an internal standard. Labelled water, D_2O, was used in determining whether the protons were exchangeable. Mass spectra were measured at 70eV. In addition, uncorrected melting points were determined.

Melting points were determined on the crystalline compounds from the urine of all the other rodent species to ascertain whether the same compound was present in all of them.

Water turnovers

Water turnover rates were monitored in a separate group of animals collected in the same areas. These animals were left to acclimate to laboratory conditions for one month prior to the commencement of hydropenia. Percentage water turnover rates (WTRs) were measured using the isotopic dilution technique (Richmond _et_ _al_., 1962; Holleman and Dieterich, 1973). Each animal was injected intraperitoneally with 10μCi tritiated water (TOH) whilst still being maintained on an _ad_ _lib_. water supply, just prior to the commencement of water stress. Water turnover rates were calculated from changes in the TOH concentration in consecutive blood samples taken at four day intervals, commencing after ten days without free water.

Blood samples were collected from the orbit as described previously. These were centrifuged for ten minutes and then the heparinised capillary tube was broken to provide a clear plasma sample. The volume of this sample was calculated from the tube length occupied by plasma and the inside diameter of the capillary tube. These samples were washed in 100µl of 10% trichloroacetic acid in order to precipitate the plasma proteins. They were then stored in Eppendorf vials for subsequent analysis. Distilled water and stock TOH samples were treated in a similar manner.

The Eppendorf vials were centrifuged to obtain a protein free supernatant, and a 50µl sample of clear supernatant was thoroughly mixed with 10ml Packard Instagel scintillation cocktail. Radioactivity was measured using a Packard liquid scintillation counter (model 3385). A Wang 700 bench top computer programmed to correct for quenching was used to convert counts per minute to disintegrations per minute. The WTR was calculated using the equations of Yousef et al. (1974).

Statistical analyses included Student's t-tests and analysis of variance according to the methods of Zar (1974).

Results

Species producing a crystalline precipitate

All members of the Cricetidae examined produced a substantial crystalline deposit in their urine when deprived of water. None of the Muridae examined excreted a crystalline waste (Plate 1).

Chemical analysis of the crystalline compound

The crystals of the precipitate in the urine of D. auricularis, G. paeba and T. leucogaster were insoluble in most of the common organic solvents with the exception of warm dimethylsulfoxide (DMSO) and dimethylformamide (DMF) and were only very slightly soluble in water. The spectra obtained from the precipitate of the three species were identical and showed no trace of impurity. The IR spectrum showed absorption at 3470 to 3370 cm^{-1} and 1785 to 1710 cm^{-1} indicating an NH group and a CO group respectively (Fig. 1).

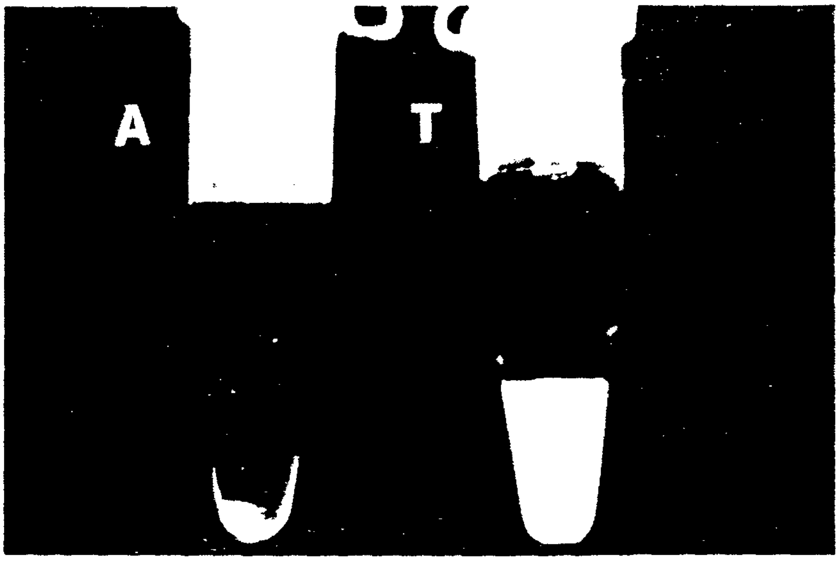

Plate 1 : Twenty-four hour urine samples from A) *Aethomys namaquensis* and B) *Tatera leucogaster* deprived of water for six weeks.

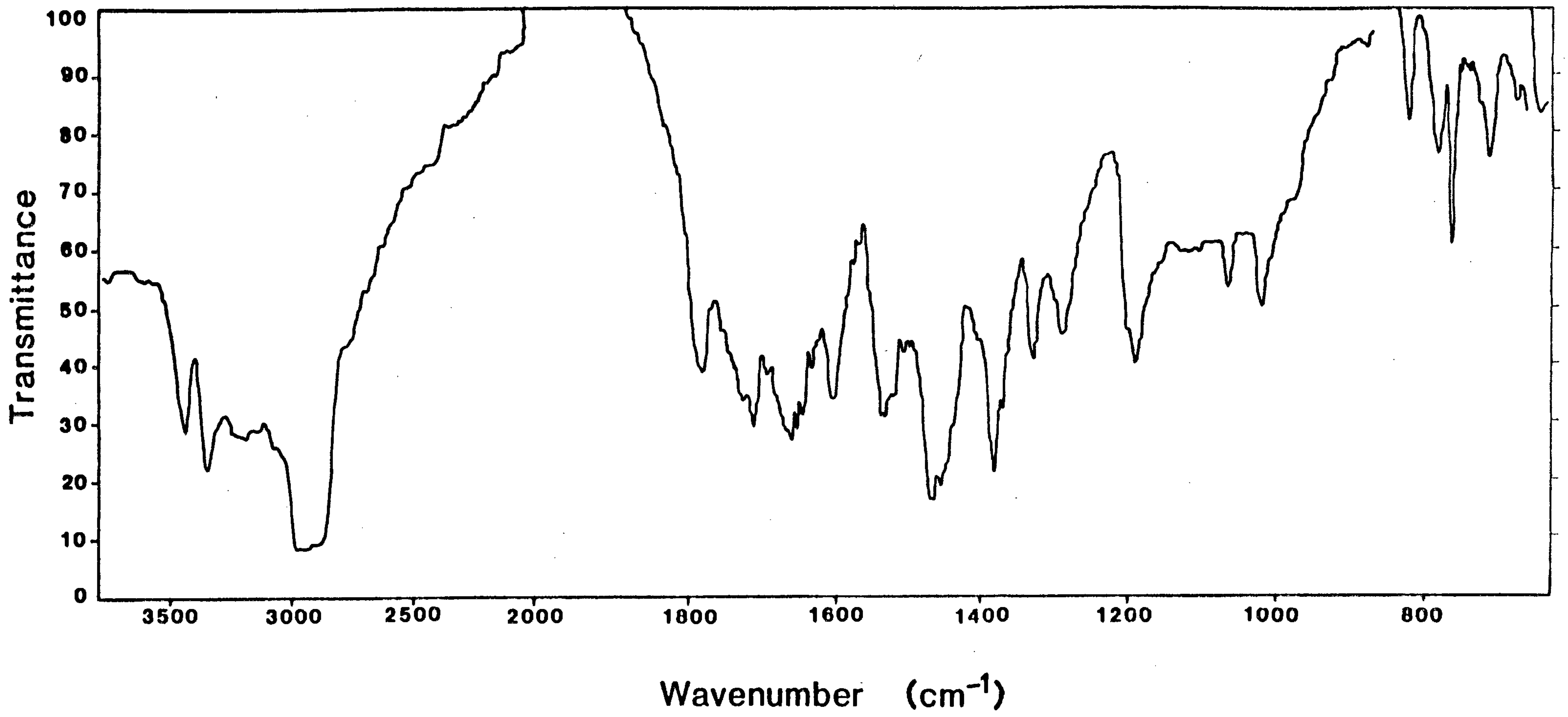

Figure 1 : IR spectrum of the crystalline component in *Tatera leucogaster* urine

The 100Mhz 1H-nmr spectrum clearly defined all six protons. The one proton singlets at d 10.34 and 8.05 were assigned to H-3 and H-1 respectively. Both were D_2O exchangeable. The one proton doublet at d 6.90 ($J_{H,H}$ = 9Hz) was attributed to H-6. The two proton doublet at d 5.78 was due to the NH_2 group and the one proton doublet at d 5.28 ($J_{H,H}$ = 9Hz) was assigned to H-5 (Fig. 2). The high resolution mass spectrum gave a molecular ion at m/e 158.04458. $C_4H_6N_4O_3$ requires m/e 158.04399. Major fragment ions were recorded at m/e 141 (M-17), 130 (M-CO), 115 (M-CONH), 87, 60, 55, 44 (Fig. 3). The crystals had a melting point of 232-233°C. Crystals from all the species that produced an off-white precipitate in their urine had similar melting points.

From the melting point and the spectral data, the crystalline compound was identified as allantoin, data agreeing closely with published values. The structure of this compound is given in Fig. 4. The spectra were pure and no other compounds were present.

Urine concentrating capacity

All arid species were quite capable of existing for fairly long periods (six weeks) without free water. Desmodillus auricularis did not lose any weight when

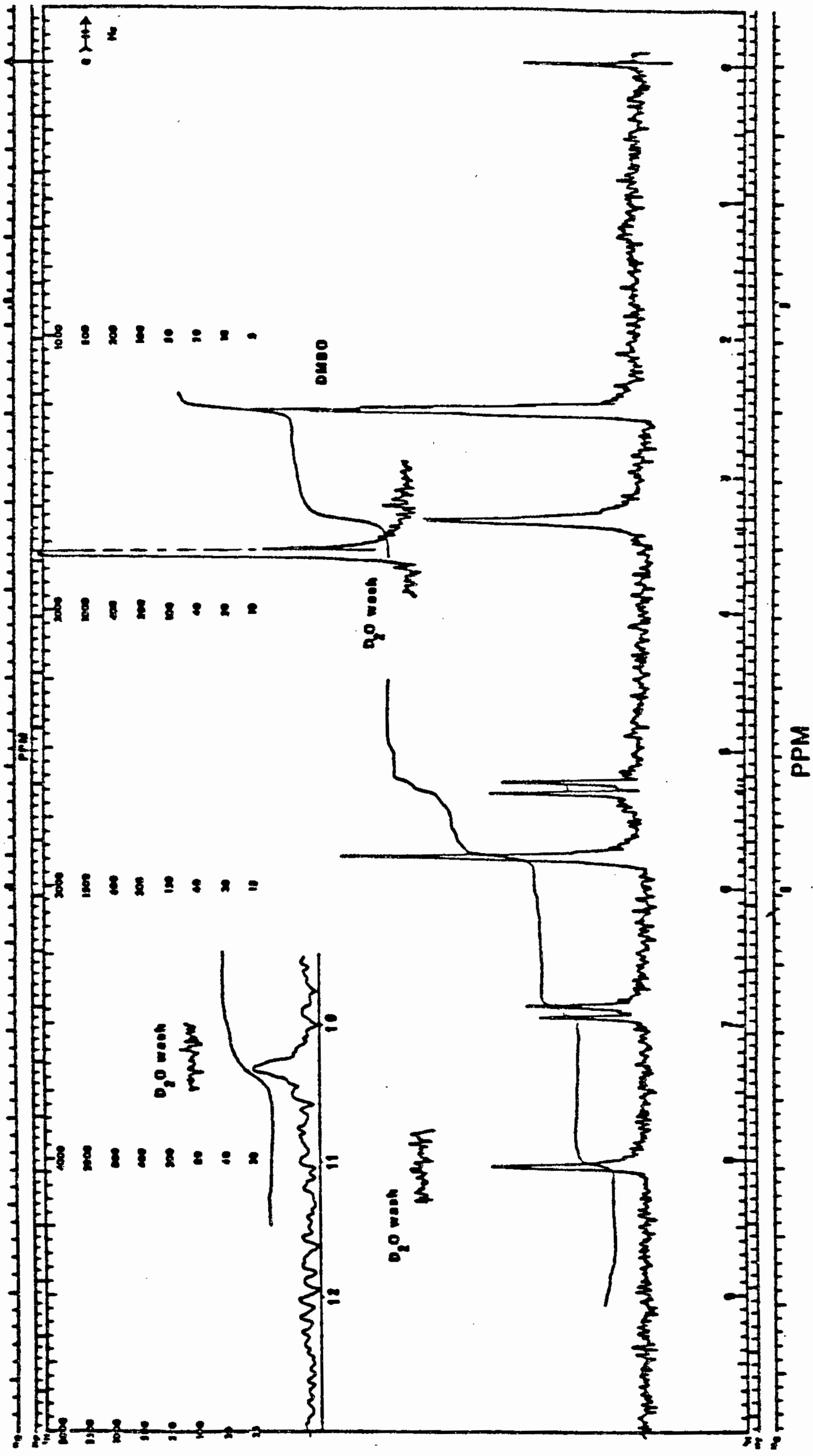

Figure 2 : 1H-nmr spectrum of the crystalline component in *Tatera leucogaster* urine

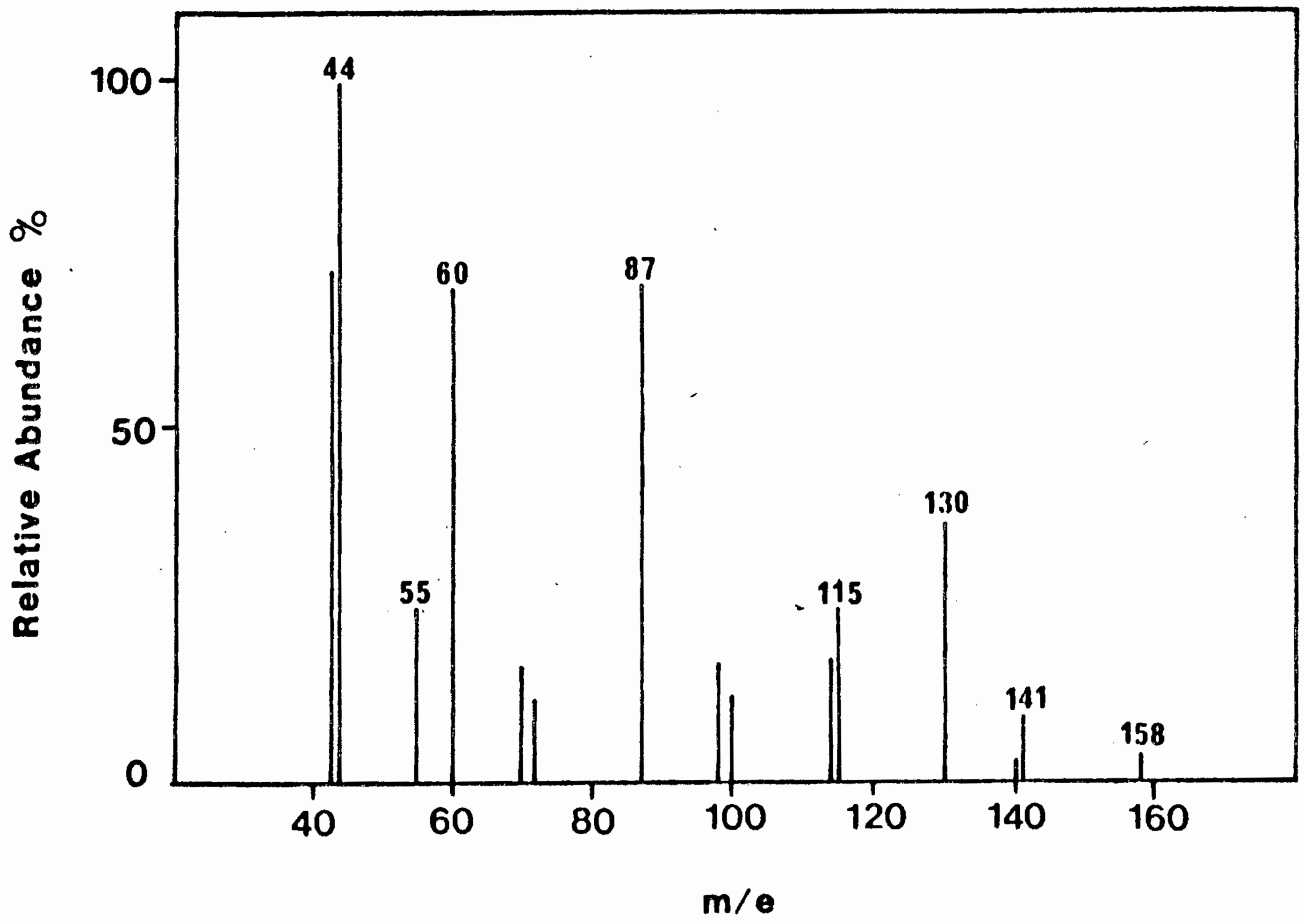

Figure 3 : Mass spectrum of the crystalline compound in *Tatera leucogaster* urine

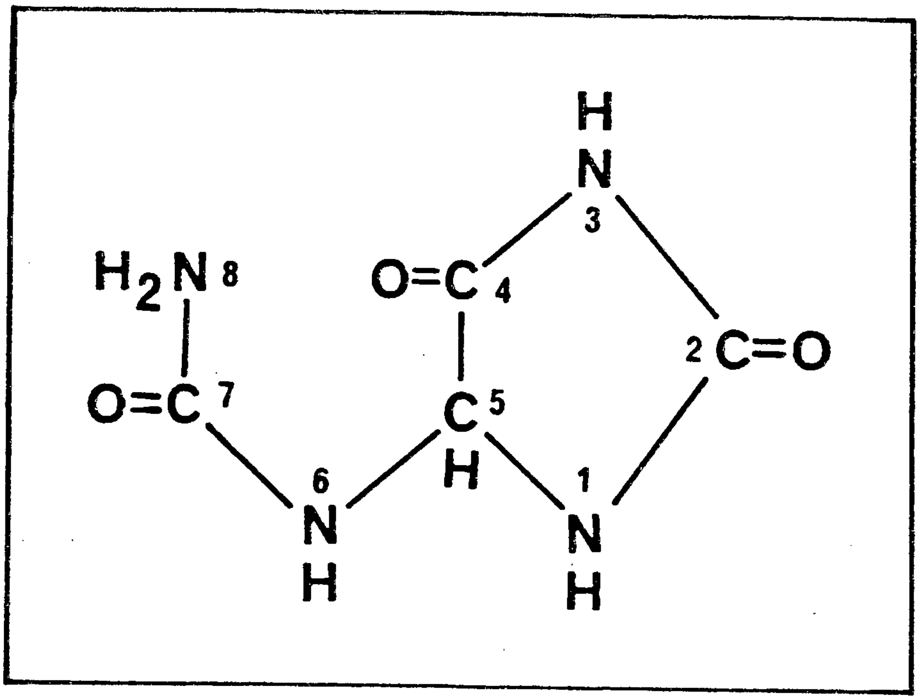

Figure 4 : Structure of allantoin

deprived of water, whereas R. pumilio lost the most (25%) before mass stabilised. All other arid-adapted species showed intermediate responses (Buffenstein, in press & prep).

Urine osmolality increased progressively over the period of water restriction reaching a maximum after one month. Desmodillus auricularis produced the most concentrated urine (5500mOsm.kg $^{-1}$) when deprived of water and also showed the highest urine/plasma (14:1) ratio (Table 1). The cricetids as a whole showed significantly higher ($p \leq 0.001$) urine concentrations (5033 ± 277 mOsm.kg $^{-1}$; n = 5) when deprived of water than the murids (3704 ± 61 mOsm.kg $^{-1}$; n = 6). Urea concentrations (Table 2) rose concomitantly with increased osmolality. Urea exerts the major influence on the osmolality of the urine in all species. Consequently the cricetids investigated had significantly higher ($p \leq 0.05$) maximum concentrations of urea (3528 ± 227.4 mM.1 $^{-1}$; n = 68) than those of the murids (2263 ± 185 mM.1 $^{-1}$; n = 2). Uric acid concentrations were also maximal with hydropenia. Both the murids (0.28 ± 0.07 mM.1 $^{-1}$; n = 2) and the cricetids (0.37 ± 0.05 mM.1 $^{-1}$; n = 7) showed similar maximum concentrations ($p \geq 0.10$).

Percentage daily water turnover rates of the two families (cricetids:- 387 ± 0.11% n = 4, murids: 5.00

TABLE 1 Maximum urine and plasma concentrations in arid-adapted rodents deprived of water for six weeks

Species	n	Concentration mOsm l^{-1} Urine $\bar{x}$	Urine ± S.E.	Plasma $\bar{x}$	Plasma ± SE	Urine/Plasma Ratio
CRICETIDAE						
Desmodillus auricularis	15	5507	339	396	16	14
Gerbillurus paeba	32	4837	178	413	12	12
Gerbillurus setzeri	14	5368	148	480	22	11
Gerbillurus tytonis	16	5404	222	456	18	12
Gerbillus pusillus	12	4084	210	505	21	9
Tatera leucogaster	30	5000	172	404	10	12
MURIDAE						
Acomys subspinosus	4	3784	186	586	18	7
Aethomys crysophilus	2	3468	372	424	22	8
Aethomys namaquensis	28	3725	136	419	14	9
Praomys natalensis	4	3740	540	400	28	9
Rhabdomys pumilio	6	3805	230	444	21	9

TABLE 2 Maximum concentrations of urea and uric acid in the urine of some cricetid and murid rodents from the Namib desert

Species	Urea concentration (mM)			Uric acid concentration (mM)		
	$\bar{x}$	$\pm$ S.E.	n	$\bar{x}$	$\pm$ S.E.	n
MURIDAE						
Aethomys namaquensis	2449	199	10	0.36	0.06	10
Rhabdomys pumilio	2077	208	13	0.20	0.03	9
CRICETIDAE						
Desmodillus auricularis	3929	149	10	0.58	0.60	7
Gerbillurus paeba	3900	491	8	0.23	0.08	5
Gerbillurus setzeri	3353	203	9	0.39	0.07	7
Gerbillurus tytonis	3169	284	8	0.21	0.09	8
Gerbillus pusillus	2351	215	15	-	-	-
Steatomys krebsii	2513	195	6	-	-	-
Tatera leucogaster	3592	911	12	0.45	0.05	13

± 0.10%; n = 2) were significantly different ($p \leq 0.02$). When deprived of water for two weeks, water turnovers of the cricetids was approximately 77% of that of the murids (Table 3).

Allantoin excretion

Considerable difficulty was experienced when assaying the quantities of allantoin dissolved in the urine. The photometric assay of Vrbaski *et al*. (1978) was found to be very sensitive to the presence of urea as is indicated by the linear relationship we obtained between urea concentration (x) and optical density (y):

$$y = 0.095 + 0.196x \ (g.l^{-1}) \qquad r = 0.99$$

Quantities of allantoin in solution were therefore estimated by subtracting the known concentrations of urea (Table 2) from the 'allantoin' concentrations determined photometrically (Table 4). The concentration of allantoin dissolved in the urine of *A. namaquensis* and *D. auricularis* fell within the solubility range of allantoin whereas the urine of *G. paeba* and *T. leucogaster* was slightly supersaturated.

Allantoin in the crystalline precipitate was found to be pure and contributed substantially to both urine mass (Table 4) and to the amount of nitrogen excreted (Table 5).

TABLE 3 Water turnover rates in rodents from the Namib desert

Species	WTR (%) $\bar{x}$	± S.E.	n
MURIDAE			
Aethomys namaquensis	4.82	0.41	21
Rhabdomys pumilio	5.18	0.43	6
CRICETIDAE			
Desmodillus auricularis	4.30	0.67	7
Gerbillurus paeba	4.01	0.74	6
Gerbillurus tytonis	3.91	0.98	6
Tatera leucogaster	3.26	0.46	11

TABLE 4 Allantoin excretion in Namib desert rodents deprived of water for four weeks

Species	Allantoin in solution**			Allantoin*	Crystalline allantoin			%
	n	mg l^{-1}	mM	mM	n	mmol day^{-1}	mg day^{-1}	Urine mass
CRICETIDAE								
Desmodillus auricularis	8	718.0 ± 71	4542 ± 449	613	9	0.35 ± 0.03	56.0 ± 5.2	29.63 ± 2.8
Gerbillurus paeba	8	742.0 ± 198	4695 ± 444	795	13	0.29 ± 0.002	45.3 ± 3.1	28.49 ± 2.1
Tatera leucogaster	11	705.3 ± 168	4463 ± 320	871	16	1.11 ± 0.43	175.0 ± 7.0	28.94 ± 9.3
MURIDAE								
Aethomys namaquensis	9	484.3 ± 168	3062 ± 355	613	28	0.00 ± 0.00	0.0 ± 0.0	0.00 ± 0.0

** Using Vrbaski *et al.*'s (1978) photometric assay

* Calculated by deducting urea concentrations from **

TABLE 5 Daily nitrogen excretion in urea and allantoin and estimated water savings by excreting crystalline allantoin instead of urea

	Aethomys namaquensis		*Desmodillus auricularis*		*Gerbillurus paeba*		*Tatera leucogaster*	
	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%	$\bar{x}$	%
Mass (g)	47.9	-	59.9	-	29.9	-	53.7	-
Urine vol. (10^{-1} mℓ day^{-1})	4.0	-	1.5	-	1.4	-	5.0	-
Total urea (10^{-3} mmol day^{-1})	979.6	79.97	550.1	55.45	443.6	52.50	1796.0	53.74
Total uric acid (10^{-4} mmol day^{-1})	1.3	0.01	0.8	0.01	0.34	0.0	2.3	0.01
Total allantoin in solution (10^{-3} mmol day^{-1})	245.2	20.02	92.0	9.27	111.3	13.17	435.5	13.03
Total allantoin solids (10^{-3} mmol day^{-1})	0.0	0.0	350.0	35.28	290.0	34.32	1110.0	33.22
Total nitrogenous wastes measured	1224.9	-	992.1	-	844.0	-	344.17	-
Nitrogen in urea (10^{-3} mg day^{-1})	27.4	66.67	15.4	28.07	12.4	35.81	50.2	36.76
Nitrogen in dissolved allantoin (mg day^{-1})	13.7	33.33	19.6	35.74	6.2	17.90	24.4	17.86
Nitrogen in crystalline allantoin (mg day^{-1})	0.0	0.0	19.8	36.18	16.0	46.29	61.95	45.36
Total nitrogen excreted (mg day^{-1})	41.1	-	54.8	-	34.6	-	136.55	-
Water saving from crystalline fraction (10^{-3} mℓ)	0.0	0.0	38.0	25.33	31.0	21.95	119.0	23.8

Discussion

Allantoin excretion

Most mammals, with the exception of the Dalmation dog and some primates, including man, excrete their purine catabolites in the form of allantoin. This is produced predominantly in the liver by hepaticuricase (Byers et al., 1947). Rattus sp. on a normal diet excrete approximately 1.5mmol.kg^{-1} body mass .day^{-1} (Greger et al., 1976). This quantity falls well within the water solubility range (6.3mmol.l^{-1}). Using tracer techniques Greger et al. (1975) showed that the renal handling of allantoin in Rattus sp. consisted of free filtration with neither reabsorption nor secretion occurring along the nephron.

To date no mention has been made in the literature of the crystalline precipitate of allantoin found in the urine of hydropenic cricetid rodents. In fact little quantitative work has been done on the excretion of allantoin. This appears to be primarily due to difficulties encountered in the use of quantitative assays for allantoin. Only non-specific photometric assays are available (Larson, 1931; Young & Conway, 1942). These techniques are cumbersome and in the present study were found to result in considerable

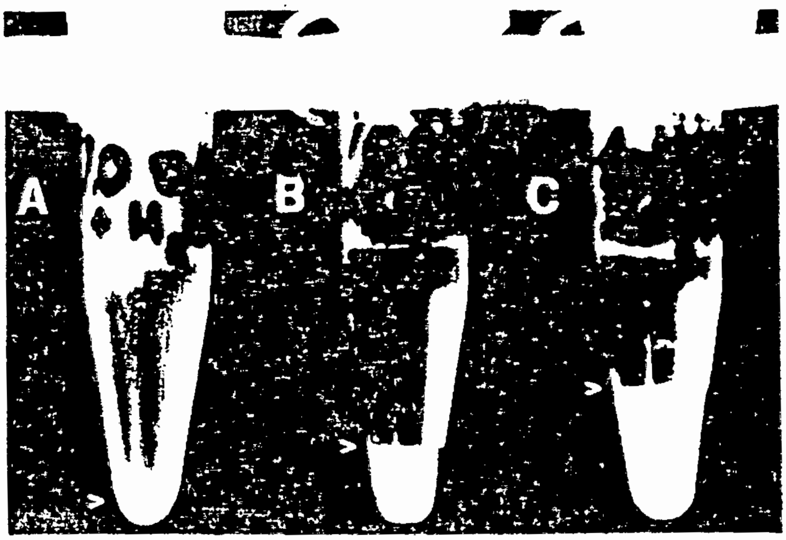

Plate 2 : Urinary crystalline deposits from an individual *Tatera leucogaster* when A) provided with *ad lib.* water, B) water stressed and C) deprived for ten days. Note the approximately three-fold increase in the amount of crystalline precipitate.

error. The main drawback of these techniques and also of more recent assays is interference from other urinary wastes, especially urea (present study, Fink *et al.*, 1963; Zelck, 1963; Pentz, 1969; Abraham *et al.*, 1976; Borchers, 1977). When using the method of Vrbaski *et al.* (1978) we found that the estimated amount of allantoin greatly exceeded the solubility range. Estimated concentrations were most unrealistic (0.5 - 1.1kg allantoin.l^{-1}). The cricetids appeared to excrete 1.5 times as much 'allantoin' as the murids. This ratio was similar to that of the urea concentrations and can therefore be attributed to urea rather than allantoin levels. From this it can be assumed that the proportion of dissolved allantoin in the urine was similar in both rodent families and this could reflect the quantity of allantoin excreted as a result of normal purine catabolism.

By contrast, the quantity of crystalline allantoin excreted by the cricetids when deprived of water (Plate 2), accounted for 29% of the daily mass of urine excreted and approximately 30% of the total nitrogen excreted per day (Tables 4 & 5). Allantoin excretion determined from the precipitate alone was substantially higher than that estimated by Pak *et al.* (1973) from body weight for rats. *Tatera leucogaster* produced 24 times (2400%) the predicted estimate for a rat of the same body mass in the solid fraction of allantoin alone. Gerbillurus paeba and D. auricularis excreted 939% and 753% respectively of that predicted by mass using the allometric equation of Pak et al. (1973).

Allantoin production in rats has been found to be influenced by several parameters: Morgan & Hanson (1964) found that larger quantities were excreted when there was an increase in protein synthesis through growth or lactation. Kiriyama & Ashida (1964) suggested that allantoin production is dependent on the age of the animal, dietary protein, body size and the rate of growth whereas Pak et al. (1973) found contradictory results. Pak et al. (1973) concluded from their experiments that the amount of allantoin excreted in the urine was independent of the age of the animal and of the diet consumed, but was directly related to a) the weight and the rate of gain in weight and b) body nitrogen content and the rate of gain of nitrogen content. Allantoin, although present in relatively high concentrations in the seeds and germinating sprouts of several plant families (Tracey, 1955; Barash, 1972), in this investigation was not present in millet seeds in any detectable quantity. In the light of these findings, it is most interesting to observe that no precipitate of allantoin occurs in the Muridae, whilst the Cricetidae, maintained on an identical diet and under the same experimental conditions, produce allantoin in quantities greater than the solubility range (Plate 1). These large quantities found cannot be merely a result of purine degradation, as the rodents used in this study were all mature, non-lactating animals which were able to survive indefinitely on a diet of air-dried seed alone. All measurements reported here were taken after mass had stabilised. Any slight changes in mass were common to both families and cannot therefore account for the differences found.

Significance of allantoin excretion

Both families are primarily ureotelic, urea constituting the major solute of the urine osmolality. Urea accounted for 67% of the total nitrogen excreted in hydropenic A. namaquensis, whereas it constituted only 28% of the total nitrogen in D. auricularis deprived of water (Table 5). By not converting allantoin to urea and glyoxylic acid, or conversely by converting urea to allantoin, three moles of water are saved for every one mole of urea (Lehninger, 1970) and this saving does not include that of reduced solvent requirements. From this one can deduce that approximately 20% of the water excreted in the liquid component of the urine is saved. This saving in water is reflected in the significantly different WTRs ($p \leq 0.001$) between the murids and the cricetids of the

Namib. The WTR saving is similar in magnitude (Table 5) to the savings calculated from the solid moiety. Cricetid WTRs were slightly lower than the most efficient WTRs recorded by Yousef et al. (1974) for heteromyid rodents. These low WTRs were accompanied by concomitantly high maximum osmolalities and urea concentrations.

Shifts in the major nitrogenous components from ammonia to urea are a common phenomenon in the lower vertebrates. Shifts in this biochemical pathway from urea to uric acid when temperatures are elevated and water limiting, have also been observed in some frogs (Loveridge 1970) and in tortoises (Drilhon & Marcoux 1942). The cricetids however, appear to be unique amongst the mammals in showing a shift from urea to allantoin.

The ability to produce a concentrated urine has been viewed as an indicator of efficiency of water conservation (Schmidt-Nielsen, 1979). Results in this study suggest that the African cricetids are more pre-adapted for desert niches than the murids. The murids are relatively recent invaders of the harsh Namib desert (Meester, 1965; Missone, 1969) and their distribution is restricted to the more mesic regions on the eastern side of the Namib, rocky outcrops and densely vegetated areas (pers. obs., Coetzee, 1969;

Christian, 1979; Withers, 1979). It is possible that markedly increased rates of allantoin excretion confer an adaptive advantage to the long-term residents (Cricetidae) of the Namib.

The generalisation that the murids are less well adapted for desert survival in the arid zones of Africa cannot be applied universally as the Australian murids hold the record for the most concentrated urine (MacMillen & Lee, 1969; MacMillen *et al*., 1972; Hewitt *et al*., 1981). Missone (1969) whilst examining the evolutionary history of the murids suggested that Africa and Indo-Australia have been separated from each other sufficiently long to allow an almost complete generic seperation. This might account for the difference in renal performance between the African and Australian murids. However, we have observed that the severity of water stress during weaning influences kidney concentrating ability in both *A. namaquensis* and in *T. leucogaster* (unpublished data). Individuals weaned without free water showed maximum urine osmolalities within the range reported for the Australian murids, whilst their litter mates weaned with an *ad lib.* water supply had maximum urine osmolalities within the range normally observed. These findings merely emphasise the caution required when using urine concentrating capacity as an indicator of adaptive renal function.

Excretion of allantoin whilst saving considerable amounts of water, is not totally advantageous, as the synthesis of allantoin results in the removal of twice as much carbon (1C/1N as opposed to 1C/2N in urea). Carbon loss is energetically linked and excretion of allantoin is therefore more costly than urea. Nevertheless, by extrapolating data (from Schmidt-Nielsen, 1979) on the energetic cost of excreting urea or uric acid, and assuming the additional energy requirements for allantoin to be mid-way between the two, the additional energetic cost of excreting allantoin is small (0.05kcal.$l^{-1}O_2$). The excretion of large quantities of allantoin can therefore play an important role in enabling the cricetids to thrive in areas inaccessible to the murids. Even mesic cricetids have retained the ability to excrete allantoin and this might therefore be used as a taxonomic tool in assigning doubtful groups of rodents to either of these families.

These findings pose several interesting questions which remain unanswered. Firstly what shifts the biochemical activity from urea to allantoin? Secondly, are the crystals of allantoin formed intrarenally and, if so, what processes are employed to enable their passage through the urinary system? Most importantly, why, with the abundance of information on renal function of arid dwelling rodents, has this phenomenon not been previously recorded? Does this suggest that this means of water conservation is unique to the African cricetids and if so, why?

Acknowledgements

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PART 6

CHAPTER 8

SUMMARY AND CONCLUSION

This thesis was undertaken to investigate some of the adaptive mechanisms employed by African desert-dwelling rodents, which enable these animals to exploit the limited available resources and to survive the physical stresses associated with their environments.

Physiological adaptation of Gerbillus pusillus.

The basal metabolic rate (BMR) of G. pusillus was 41% lower than that predicted from mass by Kleiber's (1975) equation (Chapter 1). BMR values for G. pusillus were similar to those of the North American heteromyid group (McNab, 1970). Similarity in physiological adaptation of this gerbil, and the African cricetids in general,to the heteromyids and cricetids of north America may be due in part to their similar histories as residents of arid zones since the reformation of xeric habitats in the Pleistocene. A reduced BMR, with its resulting drop in respiratory rate, not only conserves energy but has the added benefit of reducing water loss.

Water conservation is of prime importance for G. pusillus in its natural environment, where rainfall is erratic and unreliable. In the laboratory when free water was withheld, G. pusillus lost 16% of its body weight in the first two weeks. For the remainder of the 12-week experimental period, its weight stabilized at 94% of its original body weight (Fig. 1). During this period water lost through faeces, pulmocutaneous evaporation and urine was markedly less than that lost under *ad lib.* water conditions (Chapter 4). Urinary water loss showed the most pronounced decline, to 40% of the volume excreted under *ad lib.* conditions (Chapter 4). This was achieved by an improved kidney concentrating ability as indicated by the doubling of the urine / plasma ratio. Urine concentration increased progressively with hydropenia, reaching a maximum of 4000mOsm after one month without free water (Fig. 2), three times the concentration of urine produced when water was provided *ad lib.* This concentrating ability is moderate in comparison with that of other rodents independent of exogenous water (see Table 1). However, when this resulting moderate decline in urine volume is combined with the reduced evaporative water loss (as a result of low BMR), a positive water balance is adequately maintained. Table 1 and Fig. 3 show that there is a significant correlation ($p \leq 0.05$) between maximum urine concentration and BMR (expressed as a percentage of the predicted allometric value). This finding suggests that a higher basal rate of energy expenditure is needed to produce a highly concentrated urine. It is more likely though, that the conservation of energy and water are synergistic.

TABLE 1 Mean maximum urine concentration and the level of basal metabolic rates in some desert granivorous rodents

Species	BMR % Predicted*	Maximum Urine Osmolality Mean	Source
Perognathus longimembris	54	1675	Chew *et al.* 1967; MacMillen & Christopher 1971
Gerbillus pusillus	58	4084	present investigation
Gerbillurus paeba	61	4837	present investigation
Merriones hurrianae	67	3820	Goyal *et al.* 1982
Aethomys namaquensis	68	3725	present investigation
Liomys salvani	81	4000	Hudson & Rummel 1966
Dipodomys merriami	82	3990	Carpenter 1966; Kenagy 1972
Liomys irroratus	86	3820	Hudson & Rummel 1966; Christian 1978
Notomys cervinus	86	4233	MacMillen & Lee 1969, 1970
Peromyscus critinus	92	5000	Carpenter 1966
Notomys alexis	98	4772	MacMillen & Lee 1969, 1970
Jaculus jaculus	100	6500	Hooper & Hilali 1972
Leggadina hermansburgensis	104	4711	MacMillen *et al.* 1972
Jaculus deserti	106	6000	Hooper & Hilali 1972; Schmidt-Nielsen 1979
Peromyscus truei	109	4750	Carpenter 1966
Peromyscus maniculatus	110	5465	Carpenter 1966; Heisinger *et al.* 1973
Mus musculus	112	5160	Hudson & Scott 1979
Rattus norvegicus	126	5500	Collins & Bradshaw 1973; Baverstock 1976

* From the allometric calculation of Kleiber (1975)

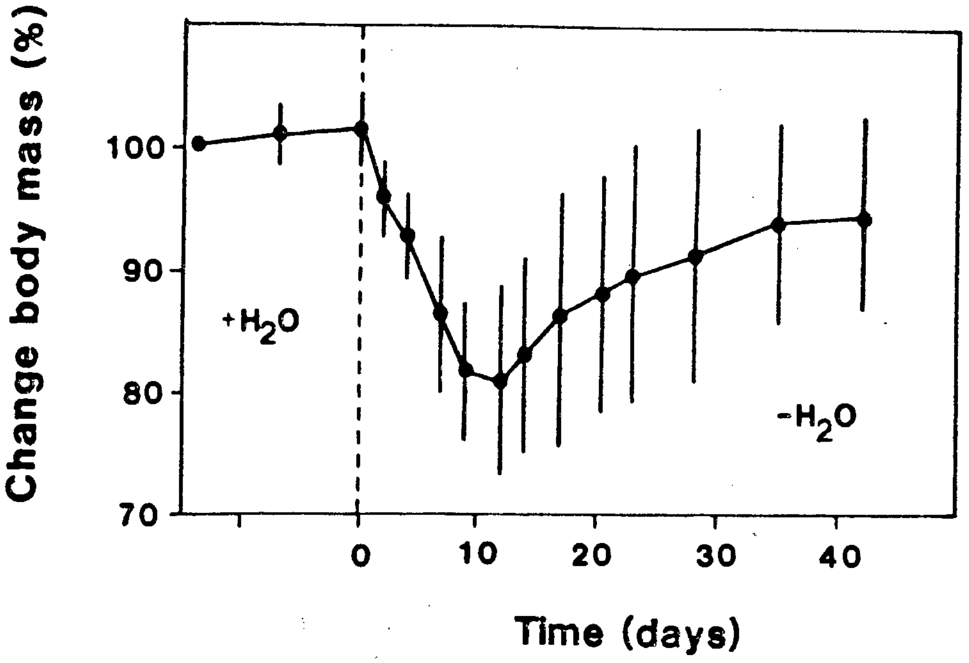

Figure 1 : Changes in body mass of *Gerbillus pusillus* over the period of deprivation of water

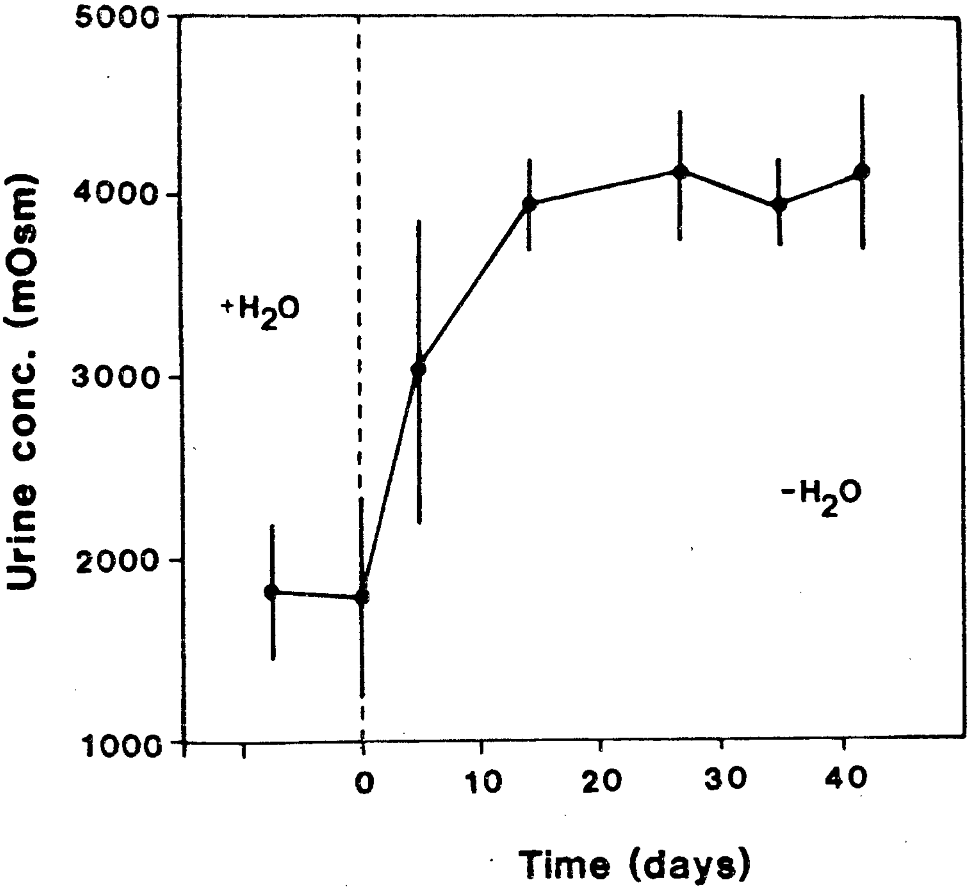

Figure 2 : Change in the urine concentration of *Gerbillus pusillus* over the period of deprivation of water

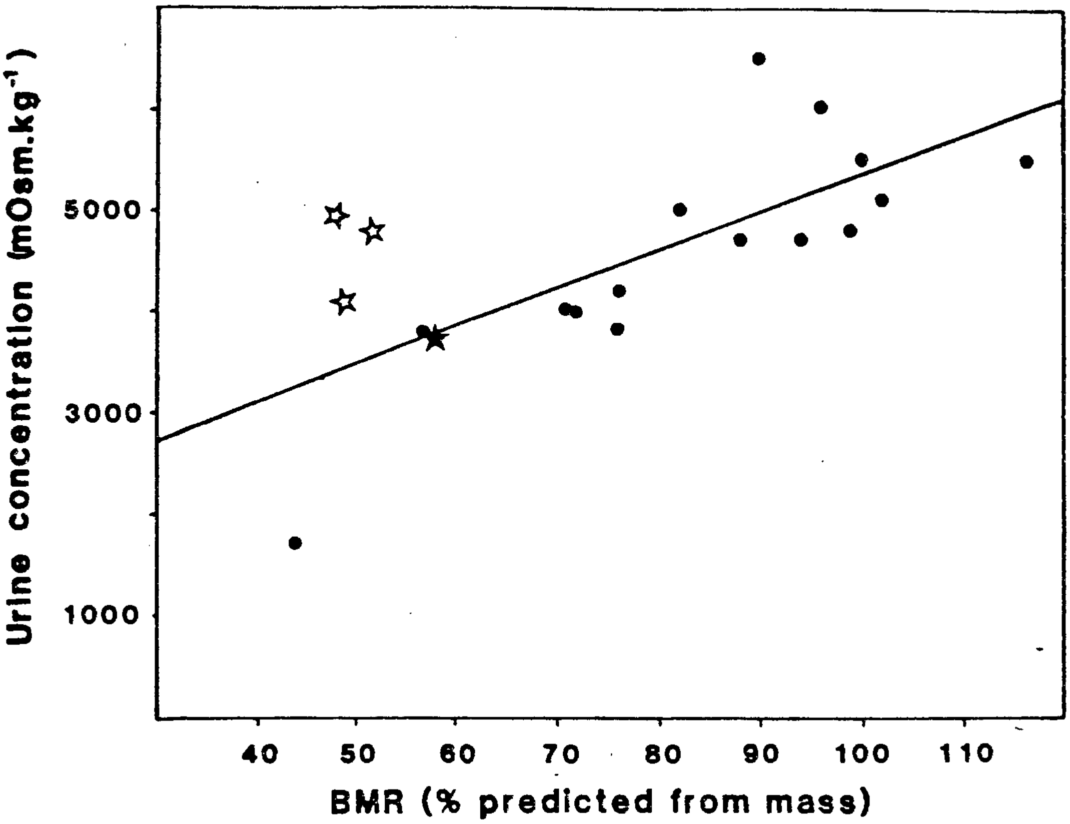

Figure 3 : Maximum urine concentrating ability and BMR (expressed as a percentage of that predicted by mass for several arid-adapted rodents (as in McNab, 1979)). Data in the linear equations used differ from those in McNab (1979) as they were taken from the original sources and some errors found in McNab's (1979) table were rectified.

☆ represent data for the cricetids and ★ *Aethomys namaquensis* from this study.

Gerbillus pusillus, when resting, has a lower body temperature (TB) than do most small mammals (Swan, 1974). This confers an energetic saving in that less energy is expended in chemical thermoregulation and also implies that shallow hypothermia is commonly employed. At temperatures below the thermoneutral zone the combined effects of chemical thermoregulation and thermal conductance maintain a fairly constant TB (+/- 2 °C). However, at high ambient temperatures, *G. pusillus* tolerates hyperthermia, having a higher lethal TB (Chapter 1) than do most other nocturnal rodents (see Hart, 1971). Use of hyperthermia by so small an animal seems incongruous, for surely the thermal inertia would be very small. However, small size renders an animal more vulnerable to all the vicissitudes of the environment and it is possible that even the small gains accrued through limited heat storage will ensure survival under circumstances which preclude the excessive use of evaporative cooling. This tolerance to stored heat with the avoidance of hypermetabolism reduces the amount of heat produced, as well as reducing water loss through evaporative cooling. At high temperatures, thermal conductance is also increased by vasodilation and behavioural means.

At less extreme temperatures, thermal conductance is lower than that predicted by mass using Aschoff's (1981) equation. This reduced conductance compensates to some extent for the low heat production and so helps in maintaining an elevated body temperature. When conductance in *G. pusillus* is compared with that of other rodents, (McNab, 1980) its value is found to be similar to that of the heteromyids and cricetids inhabiting the North American deserts.

Small mammals are compelled to compensate for the greater potential for heat exchange, by having a high metabolic rate and a low thermal conductance if body temperature is to be precisely maintained. However, as discussed above, the energetic parameters that govern precision in thermoregulation are in turn correlated with the environmental parameters of climate and food resources. Temperature regulation exhibited by this gerbil is insufficient to meet the minimum requirements for the maintenance of endothermy (Figs. 4 & 5), resulting in a fairly labile body temperature. This is also indicative of the proclivity of this species to employ hypothermia. Tolerance to labile body temperature, whilst yet another indication of careful control of resource usage, would not endanger the survival of *G. pusillus*, living as it does in the thermally stable and warm confines of a tropical desert burrow.

Despite all the energy-conserving features discussed above, when food is severely limiting (Chapters 3 & 5)

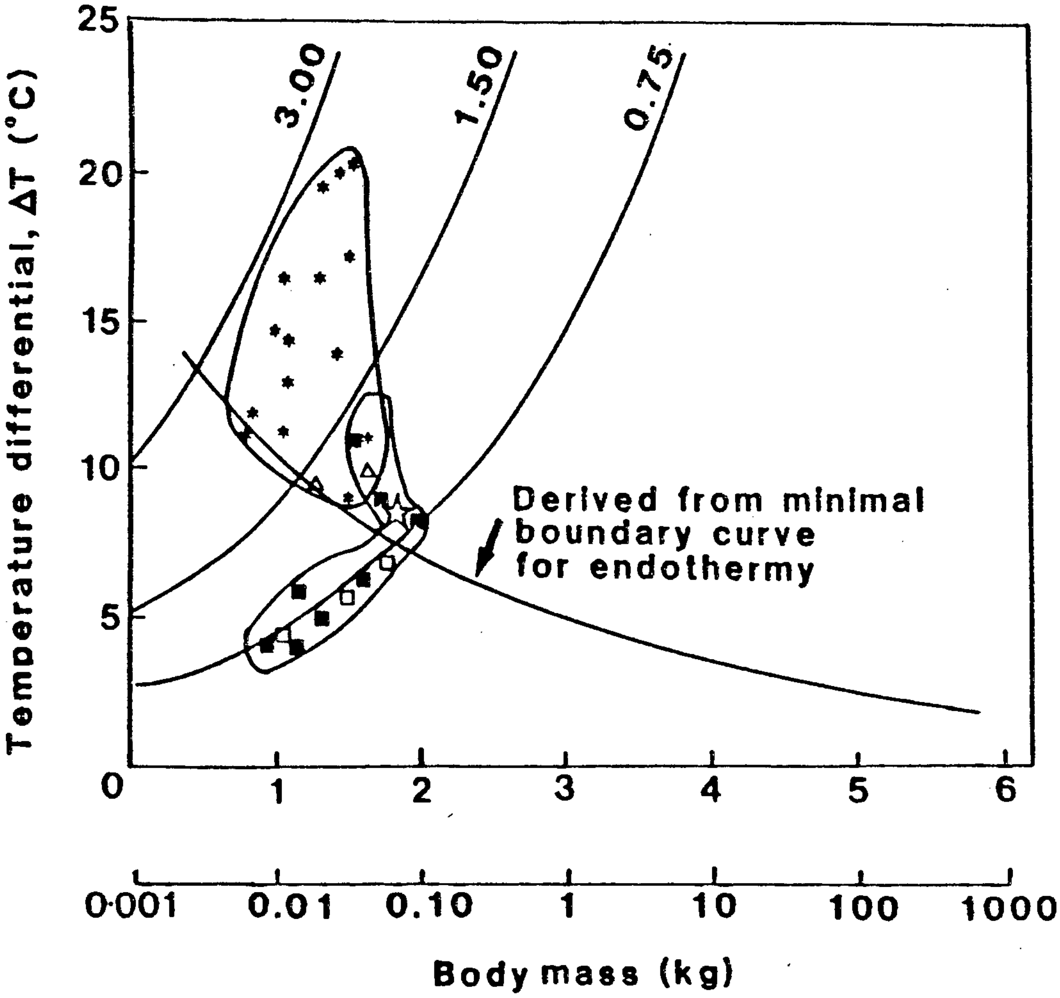

Figure 4 : Temperature differentials maintained between the body and the environment by various vertebrates. Data other than those of this investigation taken from McNab (1983). The symbols represent the following animals :

* passerines; △ shrews and moles; ■ heteromyid rodents; ☆ *Aethomys namaquensis*; and □ African cricetids.

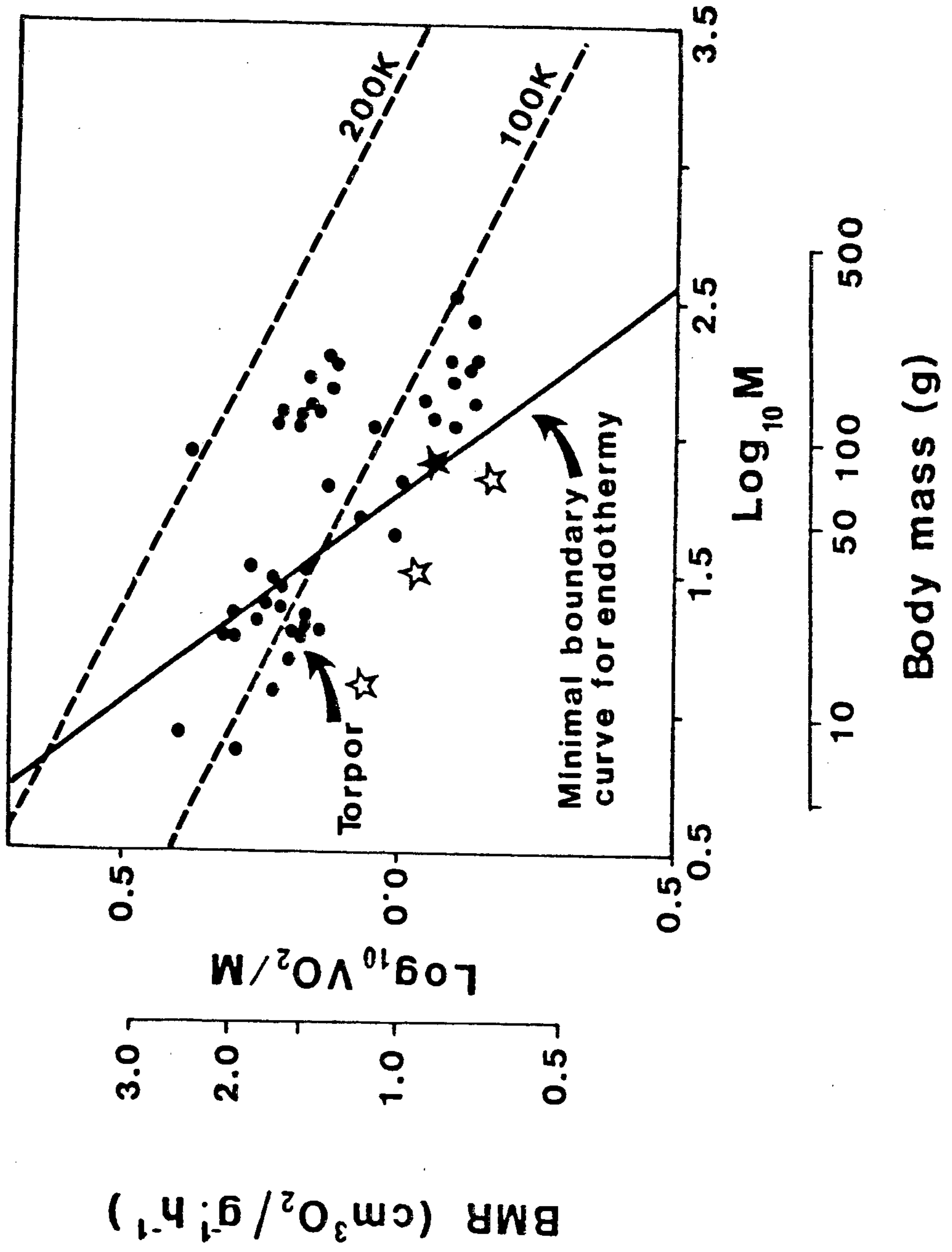

Figure 5 : Mass specific basal metabolic rates of Cricetine rodents (taken from McNab (1983) and rodents investigated in this study) in relation to body mass and the presence of torpor.

☆ represent the cricetids of this study and ★ represents *Aethomys namaquensis*.

Gerbillus pusillus exhibits bouts of daily torpor. Despite the fact that torpor is induced by inadequate food, it is a highly complex process under autonomic control (Heller and Colliver, 1974; Lyman, 1978; Hudson, 1978) and not merely a collapse in thermoregulatory ability or a primitive evolutionary remnant as suggested by Cade (1964). This is clearly demonstrated by the gerbil's ability to raise its TB back into the range of coenothermia. Facultative torpor represents a mechanism for energy conservation which has evolved in situations of high weight-specific energy demands.

Gerbillus pusillus allows its TB to drop to within 1 °C of the ambient temperature for several hours at a stretch. The critical arousal temperature from bouts of torpor was much lower (approximately 20 °C) than ambient temperatures encountered in its natural milieu, ensuring an adequate safety margin for spontaneous arousal. Above this critical temperature, arousal commences at the onset of the scotophase, enabling the gerbil to leave the burrow to forage. If an inadequate food supply were collected during foraging, the animals would again become torpid on returning to their burrows.

The duration of these torpid periods appears to be precisely controlled by the amount of food available

(Chapters 2 & 3), enabling the maintenance of a constant body mass. Sibly (1981) suggests that, given a particular diet, an animal may feed in such a way as to maximise the energy extracted from the food or may reach an optimal compromise between the requirements of digestion and the functions an animal has to perform. It was found to be more expedient for food-stressed G. pusillus to tolerate a reduction in the 'apparent assimilation efficiency' and the concomitant decline in the energy extracted from the diet rather than to expend the energy required to maintain TB in the coenothermic range for the full duration of digestion. The cost of employing torpor as calculated from the reduced AE of the food ($0.5kJ.day^{-1}$) was, indeed, insignificant in comparison with the savings accrued by the use of torpor ($32.25kJ.day^{-1}$).

In the wild, food scarcity goes hand in hand with water shortage. Water-deprived torpid gerbils voided only 4.7% of the volume of urine excreted by coenothermic water-deprived gerbils. The urine however, was not as concentrated. This is probably because fewer wastes need to be excreted and there is a proportional increase in the amount of water channelled into urine as a result of the marked decrease in pulmocutaneous evaporative water loss at the lower TB.

When food is not limiting, energy intake is slightly greater than that predicted from the allometric equation of Grodzinski and Wunder (1975). Energy expenditure, as monitored by oxygen consumption, was slightly less than that predicted (Chapter 3). Whilst this could merely reflect a difference in experimental technique, it could also indicate that G. pusillus exploits an abundance of food and water, channelling the energy over and above maintenance requirements (in this case approximately 10%) into fat stores or reproduction. In the laboratory this was most pronounced when ad lib. food and water were supplied at the end of the experiments in which food and water were restricted. During that post-experimental period, most animals appeared to become reproductively active. In the natural environment, breeding would be synchronised with the onset of the rains and the availability of new resources, enabling the first young to be weaned during the flush of new grasses and seeds (Poulet, 1972). The control of resource allocation by G. pusillus has constituted an important selection pressure. These gerbils are able to maximise optimal conditions and sit out unfavourable times, thus ensuring their success in an environment excluding many other rodent species.

Eco-physiological adaptations in Namib rodents.

Physiological adaptations controlling resource allocation often reflect the different evolutionary histories, taxonomic affinities and microhabitats of the animals concerned. Members of both the Muridae and Cricetidae inhabit the Namib desert. Thermoregulation, daily energy expenditure, water balance and renal efficiency were therefore compared so as to elucidate physiological attributes, if any, which may be explained in terms of these differences.

All Namib species examined showed adaptations to aridity similar to those of G. pusillus and other desert rodents in that resources were used sparingly and their BMRs were lower than those predicted by mass in both families (Chapter 5).

There were significant differences, however, between cricetids and murids in thermoregulatory control. The murid Aethomys namaquensis controlled body temperature precisely, whereas the cricetids, Desmodillus auricularis*, Gerbillurus paeba, Gerbillurus setzeri and Tatera leucogaster* showed a greater proclivity towards labile body temperatures. This was confirmed when temperature differentials (VO_2/Cm) for A. namaquensis, G. paeba, G. pusillus and T. leucogaster* were plotted against body mass (Fig. 5, modified from McNab, 1983).

*unpublished data

Of the four species examined, only *A. namaquensis* showed a temperature differential above the minimum required for maintenance of endothermy. Data from oxygen consumption confirm these findings (Fig. 4). This lack of precise temperature regulation in the cricetids reflects a propensity for hypothermia when conditions are stressful. This inclination was confirmed and demonstrated experimentally by maintaining four cricetid species on stressful diets. Withers *et al*. (1980) reported that one individual of *A. namaquensis*, caught in a trap in winter, had a body temperature of 19°C. Whilst this might reflect an incidence of the employment of torpor not apparent from thermoregulatory data (Fig 5 & 6), it could merely indicate that this animal was close to death.

The significant differences in thermoregulatory control and in thermal conductance found between the murid, *A. namaquensis* and the cricetid, *G. paeba* (Chapter 5) might also reflect the markedly different humidity and temperature regimes in their micro-niches. *Aethomys namaquensis* shelters in open crevices on the rocky outcrops of the Namib while *G. paeba* is fossorial. When resting, *A. namaquensis* is therefore subjected to larger diel ranges in temperature and experiences considerably lower humidities than does *G. paeba*, for its environment is not completely insulated from the effects of changes in ambient temperature, convection

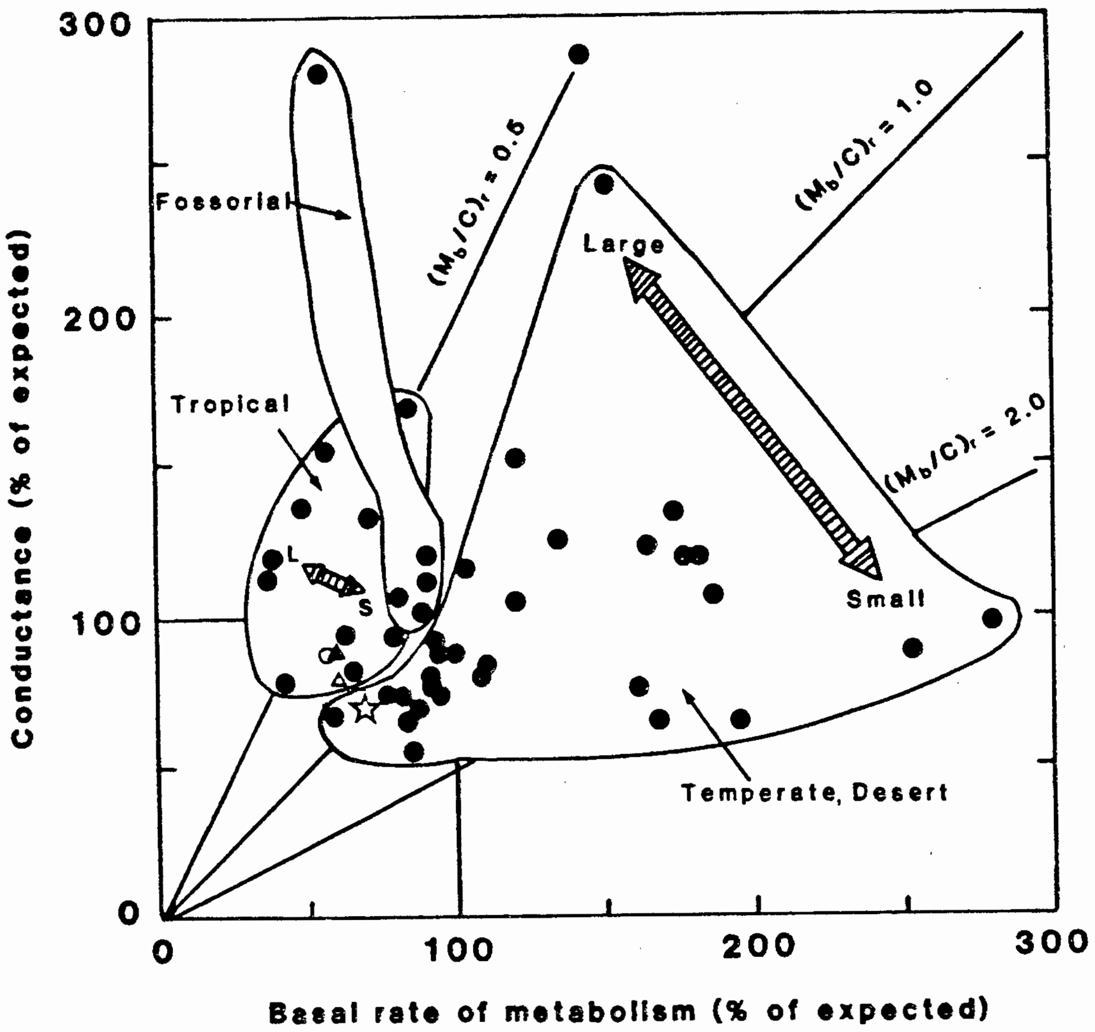

Figure 6 : Thermal conductance in mammals and birds as a function of the basal rate of metabolism.

● represent data taken from McNab (1983).

Other symbols represent values obtained in this investigation :

☆ *Aethomys namaquensis*	△ *Gerbillurus paeba*
▲ *Gerbillus pusillus*	○ *Tatera leucogaster*.

Each parameter is expressed as a percentage expected from weight in mammals.

and radiation. Thermal conductance values are therefore similar to those of animals inhabiting the temperate and desert areas where temperature fluctuations are considerable (Fig. 6). The burrow dwelling cricetids exhibit rates of conductance similar to those of animals inhabiting the tropical zone (Fig. 6). Precision of thermoregulation is not of the utmost importance at the fairly high temperatures G. paeba normally encounters when resting. Evaporative water loss is impeded by the high humidities of the plugged burrow and these rodents therefore rely mainly on a high rate of thermal conductance for the removal of heat produced during metabolism. This nocturnal burrow-dwelling animal seldom, if ever, experiences the extreme temperatures or large diel temperature ranges characteristic of desert environments. It is therefore not adapted for coping with the high temperature ranges it was experimentally subjected to, and is less tolerant of temperature fluctuations than is A. namaquensis. The microclimate experienced by A. namaquensis therefore imposes different constraints and this species copes with the fluctuations it encountered in its natural milieu by precisely controlling body temperature. It does this by compensating for its reduced BMR with a low rate of thermal conductance. This reduced heat loss at low ambient temperatures whilst enabling a reduction in heat gain at temperatures within the TNZ. These responses to the different microclimates were apparent in Fig. 6 where F ratios for the fossorial G. paeba, G. pusillus and T. leucogaster fell within the thermally stable 'tropical' group, whereas the more variable climate experienced by A. namaquensis resulted in its F ratio falling within the "temperate and desert" group.

Aethomys namaquensis lost less water than G. paeba through evaporation (Chapter 6 & 7). This difference in EWL can also be attributed to micro-climatic differences, compelling A. namaquensis to reduce EWL by morphological and behavioural means. Evaporative water loss in the confines of a highly humidified burrow does not pose a serious threat to the survival of G. paeba.

Like most arid-dwelling rodents (Reichman, 1981) both species were found to consume a fair proportion of seed in their diet. Both species had assimilation efficiencies approaching a physiological maximum. Daily energy expenditure of A. namaquensis when maintained on a millet diet was similar to that predicted by mass for a granivorous rodent, however although the DEE of G. paeba was higher than that predicted, reflecting both a certain degree of hyperactivity in captivity and the propensity of this species to supplement its diet with insects. The DEE of G. paeba fell within the predicted range for insectivorous rodents of similar mass.

Both species showed similar adaptation to aridity in that they could survive indefinitely without an exogenous water supply when maintained on a seed diet. The ability to survive periods of hydropenia can be attributed mainly to reduced urinary water loss and also to reduced evaporative and faecal water loss. *G. paeba* had an IDW of 1.3 (Chapter 6), indicating that it derives enough water from its food to enjoy a positive water balance when deprived of water, whereas, the IDW of *A. namaquensis* (0.6) implies that this species could not theoretically maintain a positive water balance. The difference in IDW reflects differences in the proportion of water lost through urine, for faecal water losses were similar and low as is typical of arid-adapted rodents. Despite differences in IDW, *A. namaquensis*. was found to survive fairly long periods of water stress (Chapters 6 & 7). It was able to do this primarily through reductions in EWL and by tolerance to haemoconcentration.

When the highly digestible diet of millet was replaced with a more fibrous diet of bran, neither species could maintain a positive water balance and, despite an attempt by *G. paeba* to reduce food consumption by employing torpor, both species succumbed to the severe water stress imposed by this diet. Reduced assimilation efficiency, and the concomitant increase in the quantities of faeces produced, resulted in a marked increase in water loss through faeces, thereby precluding the maintenance of a positive water balance. This finding stresses the importance of food selection. Gerbillurus paeba, like the cricetids in general, was found to be more selective in diet especially when water was limiting (Chapter 6). Aethomys namaquensis, on the other hand, is fairly representative of the murids, in that it is an opportunistic feeder and was not particularly selective in its diet even in times of water stress. Consequently, when water is limiting, this and other species of murid should experience a higher mortality rate than would the cricetids.

Another factor which probably influences the reportedly lower mortality rates (Christian, 1979; Withers, 1979) of the Cricetidae is the excretion of large quantities of crystalline allantoin when water stressed. The quantity of allantoin excreted was far greater than that expected from purine catabolism and it appears therefore that there is a shift in the biochemical pathway of protein degradation from urea to allantoin. Excretion of allantoin would confer an ecophysiological advantage to these animals in that considerably smaller quantities of water need be lost during its excretion. This reduction in water loss was confirmed by significantly lower water turnover rates and higher urine concentrations.

It is not known why all the cricetid species examined in this study produce a crystalline precipitate of allantoin while not one species of murid was found to do so. It can only be concluded that this phenomenon reflects a taxonomic difference and that it is of evolutionary advantage to the cricetids in their arid environments. The murids are thought to be more recent invaders of the arid zones of Africa and may therefore not have been subjected to the same extent to the selection pressures of arid environments. These animals therefore still have a fairly restricted distribution in the arid regions of Africa and are compelled to compensate for their incomplete adaptation to these harsh environments by channelling more energy, when times are favorable, into reproduction.

The cricetids are generally 'low equilibrium' species (ie K-selected; Pianka, 1970) with low reproductive rates and low mortality rates. Problems of resource usage are to a large extent ameliorated by expending slightly more energy on the excretion of a more insoluble nitrogenous waste, allantoin, when water is limiting, and by resorting to energy-conserving torpor when food is limiting. These combined methods of resource management ensure the continuous survival of these species in the arid zones of Africa. Murid survival in the Namib is not guaranteed, for these animals could be completely eliminated from this area by too many successive years of drought.

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