SELECTED ASPECTS OF THE ADAPTIVE BIOLOGY AND ECOLOGY OF THE NAMIB DESERT GOLDEN MOLE (*EREMITALPA GRANTI NAMIBENSIS*)

by

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THIS WORK IS DEDICATED TO MY FATHER

AND TO THE MEMORY OF MY MOTHER AND MY GRANDMOTHER

PREFACE

The work described in this thesis was carried out at the Desert Ecological Research Unit, Gobabeb in the Namib Desert and in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg, from March 1983 to July 1989, under the supervision of Professor M.R. Perrin and Professor G.C. Hickman.

These studies represent original work by the author and have not been submitted in any form to another University. Where use was made of the work of others, it has been duly acknowledged in the text.

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ABSTRACT

Eremitalpa granti namibensis is a small blind subterranean insectivore (Chrysochloridae) endemic to the Namib Desert sand dunes. This study of the biology and ecology of the Namib mole assesses its adaptive strategies for survival in a harsh environment. Major areas of study include feeding ecology, movement patterns, home range, activity, thermoregulation and water metabolism.

Diet of free-living moles was assessed through stomach content analysis while qualitative and quantitative descriptions of surface foraging paths related searching behaviour to resource abundance and distribution. Moles opportunistically fed on termites, a sedentary prey resource occurring in patches of high concentrations while non-random surface locomotion minimised foraging costs.

Population density and home range utilisation were studied by following surface trails and capture mark and recapture. Population density was low but stable and home range size large. No permanent nests or burrows were found while the pattern of home range utilisation was nomadic but circumscribed.. Although ranges overlapped, a system of mutual avoidance limited encounters with neighbouring animals.

Activity phasing was examined in the field and in the laboratory. Free-living moles were almost exclusively nocturnal while captive moles were active day and night.

These findings are discussed in relation to prey availability, predator pressure and avoidance of diurnal extremes. Light and temperature appeared to be important cues for daily onset and cessation of activity.

Aspects of thermoregulation examined under laboratory and field conditions revealed high thermal conductance, a low basal metabolic rate and poor thermoregulatory abilities. Factors suggested to have selected for these traits are the gaseous regime of the sand in which moles burrow and the need to minimise energy expenditure in an energy sparse environment.

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

In summation, a broad overview of adaptive radiation in Namib moles compared to other subterranean mammals is discussed.

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CHAPTER 1

INTRODUCTION

BACKGROUND AND AIMS

The African golden moles (Chrysochloridae) are blind, solitary subterranean insectivores endemic to Africa, south of the Sahara (Smithers, 1983). A general review of chrysochlorids is given by Hickman (in press). Fossil remains are known as far back as the Lower Miocene in Kenya (Butler & Hopwood, 1957) showing that contemporary members have changed very little in their morphology over geological ages. Uniformity of morphological features through the family (Dobson, 1882; Kingdon, 1974), associated with specialisation for an almost exclusively fossorial mode of existence, belies the wide geographic range of habitats both climatically and altitudinally occupied by various species (Fig. 1.1). In southern Africa, golden moles are distributed throughout all four major biotic zones: the south west arid zone; forest (montane and subtropical); the southwest Cape (Cape macchia) and southern Savanna (Meester, 1965). Further north, records of golden moles are more scattered and often restricted to mountains and mountain ranges (Duncan & Wrangham, 1971; Jarvis, 1974; Lamotte & Petter, 1981).

Although the distribution of the Chrysochloridae is characterised by great ecological variation, little attention has been devoted to the physiological and behavioural characteristics which enable different species to function

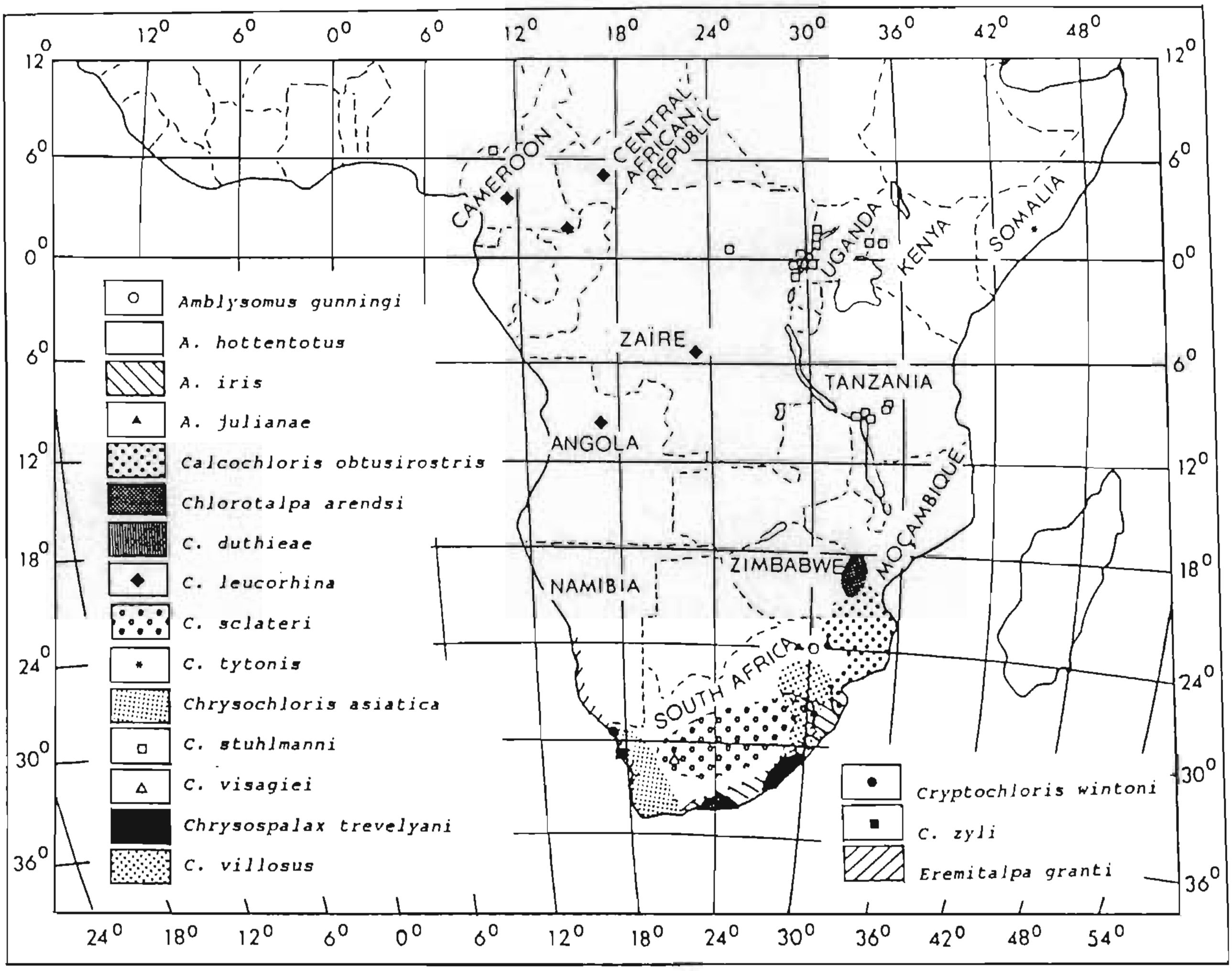


FIGURE 1.1: The distribution of chrysochlorids. Reproduced from Hickman (*in press*).

efficiently within a particular habitat. Aspects of behaviour and ecology have been studied in detail in only one species, the Hottentot golden mole, (*Amblysommus hottentotus*) (Kuyper, 1979, 1985; McConnell, 1986), while limited information is available for the giant golden mole (*Chrysospalax trevelyani*) (Poduschka 1980, 1981, 1982; Duckworth & Hickman, 1985; Maddock, 1986; Maddock & Hickman 1985), the Namib Desert golden mole (*Eremitalpa granti namibensis*) (Holm, 1969), and the East African golden mole (*Chrysochloris stuhlmanni*) (Duncan & Wrangham, 1971; Jarvis, 1974; Kingdon, 1974). Physiological studies are restricted to an examination of thermoregulation in the Cape golden mole, (*Chrysochloris asiatica*) (Withers, 1978) and *A. hottentotus* (Korn, 1986; Kuyper, 1979, 1985).

In contrast, European and North American subterranean mammals (insectivorous and herbivorous) have been studied extensively (see Dubost, 1968; Ellerman, 1956; Nevo, 1979; Yates & Pederson, 1982), much of this work centring on adaptive convergence of unrelated taxa in size structure and function to the physical and biotic structures of the underground environment. Not surprisingly, as Hickman (*in press*) stresses in his comprehensive review of adaptation within the Chrysochloridae, there remains 'a substantial need for basic studies on all aspects of the biology of the chrysochlorids which in turn will provide a more balanced and important broader perspective of adaptation and radiation in subterranean mammals'.

For these reasons, an ecological study of the Namib Desert golden mole, (*E.g. namibensis*), was undertaken, as representing one of the more specialised species in the Chrysochloridae, in that it is an inhabitant of the harsh arid sand dune environment of the Namib Desert. Deserts represent an unusual habitat for any insectivorous mole, since no arid or semi-arid dwelling forms are represented in the widely distributed species of Talpidae in North America, Europe and Asia (Nevo, 1979; Yates & Pederson, 1982), although the poorly studied marsupial mole (*Notoryctes typhlops*) inhabits sand dune deserts in Australia (Corbett, 1975; Howe, 1975).

This study is an assessment of the adaptive strategies of *E.g. namibensis* to the physical and biotic structures of the Namib Desert dune environment. Since the adaptive pattern of an organism involves a combination of morphological, physiological and behavioural mechanisms, the approach of this study has been broad-based, in an effort to present a holistic view of the interaction of *E.g.namibensis* with its environment. This work is by no means definitive, but is seen as forming the basis for more intensive future studies.

The main aims of the study were to investigate feeding ecology and foraging behaviour, movements and home range, activity phasing, thermoregulation and water metabolism, and hence the key facets of the adaptive biology of the Namib mole.

These sections are preceded by a synopsis of the taxonomy, morphology, distribution and ecology of *E.g. namibensis*, followed by a general description of the study area together with a short methodological description of procedures that are common to all parts of the study.

Following the major sections is a general summary and conclusions comprising a broad overview of adaptive radiation in *E.g. namibensis* in comparison with that of other subterranean mammals.

TAXONOMY

According to Meester, Rautenbach, Dippenaar and Baker (1986), there are currently seven genera and 18 species of golden moles, although some uncertainty concerning relationships between genera does exist, resulting in several disparate taxonomic view points (Ellerman, Morrison-Scott & Hayman, 1953; Meester *et al*., 1986; Petter, 1981; Roberts, 1951; Simonetta, 1968). The genus *Eremitalpa* Roberts, 1924 contains only one species, *Eremitalpa granti* (Broom, 1907) which at present is divided into two subspecies listed by Meester *et al*. (1986) as:

Eremitalpa g. granti (Broom, 1907)
Eremitalpa g. namibensis (Bauer & Niethammer, 1959)

Eremitalpa g. granti includes *E.g. cana* of earlier authors (Meester, 1964, 1971). Bauer and Niethammer (1959) speculated that *E.g.namibensis* might be a synonym of *Chrysochloris damarensis* Ogilby (1838), which has not again been collected since the time of its original description from Damaraland. Meester (1964) has shown that this is unlikely to be the case.

Subspecies recognition rests on skull dimensions (breadth/length index) and hair length with E.g. namibensis having shorter, broader skulls and shorter hair than E.g.granti (Meester, 1964).

MORPHOLOGY

Eremitalpa granti is the smallest of the Chrysochloridae (Smithers, 1983). Measurements taken from adult E.g. namibensis caught during this study are presented in Table 1.1. Some degree of sexual dimorphism in size and mass of adult animals is apparent with females being generally smaller than males.

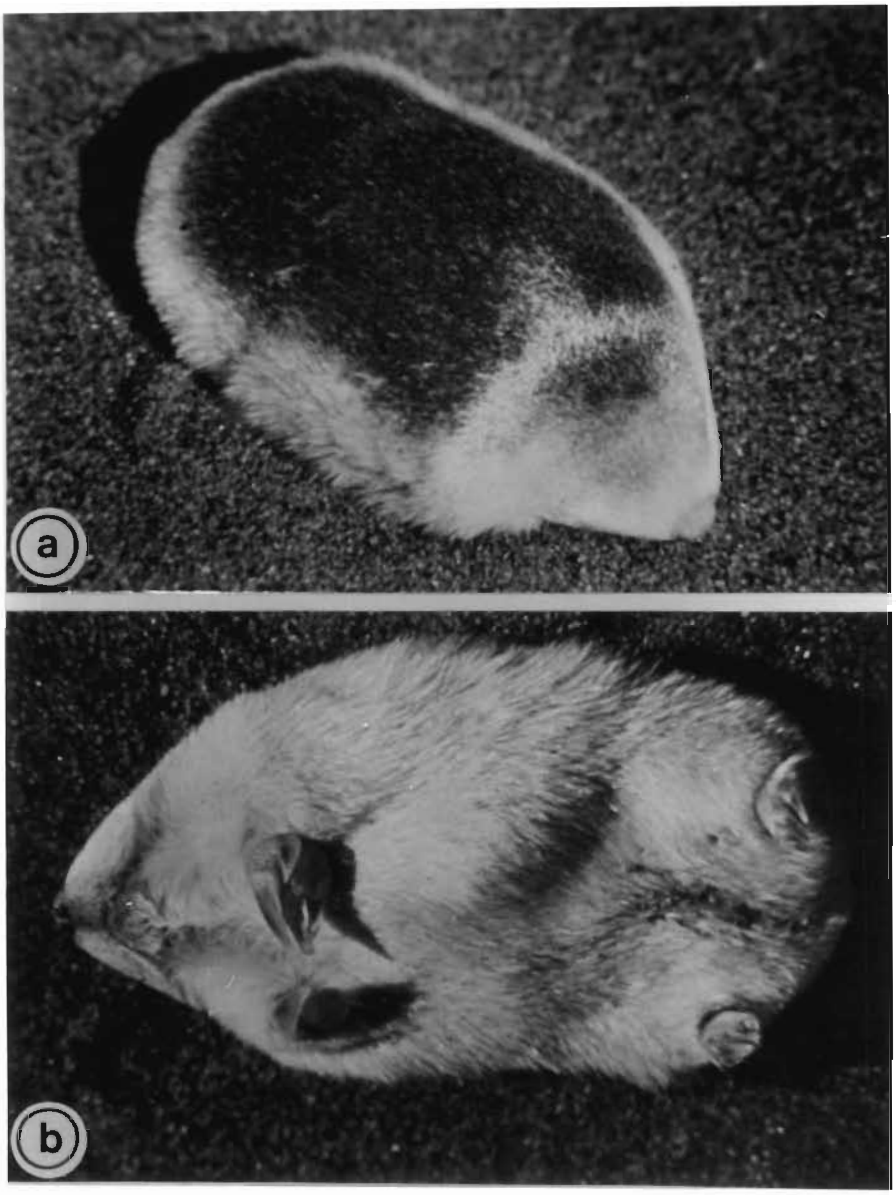
Colour is yellow and grey, with sides, abdomen and legs pale cream to yellow and the dorsal side grey (Plate 1.1a). The upper parts of the body have an iridescent silvery sheen.

General body shape is ventrodorsally flattened and fusiform with no externally visible tail. The limbs are short and medially situated beneath the body (Plate 1.1b) with the forelimbs highly adapted for burrowing. The foreclaws on the first second and third digits are extremely long, broad and hollowed out ventrally, an adaptation to burrowing in loose sand (Smithers, 1983). Details of the functional morphology of the locomotor system are given by Gasc, Jouffroy and Renous (1985), who concluded that E.g. namibensis does not depart significantly, as far as the musculo-skeletal system is

TABLE 1.1: Body mass(g) and standard measurements(mm) of *E.g. namibensis*

	Males (n=17)		Females (n=23)	
	$\bar{X}$	Range	$\bar{X}$	Range
Total length	73.5	65-81	66.8	60-74
Hind foot S.U.	7.9	6-10	6.9	6-8
Mass	25.3	17-30	19.8	15-23

PLATE 1.1: Dorsal (a) and ventral (b) view of *E.g.* *namibensis*.


a
b

concerned, from other chrysochlorids. Rather, the strikingly modified locomotor system of chrysochlorids (parasagital head-and-forelimb diggers) is well adapted for digging in various types of terrain without further specialisation.

The muzzle terminates in a hard leathery pad which protects the nostrils and assists in sand excavation. Nolte (1968) has described the general morphology of the nose which includes specialised features to prevent sand entering the nasal tracts.

The mouth is situated ventrally. Internal features including the soft palate and the tongue are discussed in Nolte (1968).

Dental formula is - I 3/3 : C 1/1 : P 3/3 : M 3/3 (Meester, 1964).

The eyes of adult _E_._g_. _namibensis_ are not visible externally. A rudiment can be seen under the skin, embedded in connective tissue. The vestigial eye structure of _A_. _hottentotus_ and _C_. _asiatica_ has been described by Sweet (1909). The retina is well defined, but the iris, lens and optic nerve are degenerate and the eye muscles are absent. A small coiled duct runs from the lacrymal glands, situated at the back of the eye, to the exterior. Studies by Gubbay (1956) of eye structure development in _E_. _granti_ indicate a condition closely resembling that of _A_. _hottentotus_ and _C_. _asiatica_.

Lacking pinnae, the external ear opening is concealed by hair which prevents sand entering the auditory canals. Some details on internal ear structure in *E. granti* are given in Findlay (1944) and Broom (1950), while Nolte (1968) deals specifically with *E.g. namibensis*. Of interest is the enormous size of the epitympanic recess which houses a disproportionately large malleus, suggesting that *Eremitalpa* is particularly sensitive to vibrations (Nolte, 1968).

In both sexes, the urinogenital system has one opening. In the male the testes are abdominal and the penis is located within the cloaca. The penis can be extruded by gently pressing at the base of the urogenital opening. One pair of thoracic and one pair of inguinal mammae are present in chrysochlorids (Dobson, 1882; Kuyper, 1979). In this study, only the inguinal mammae were noted in some specimens.

Studies on placentation (Gabie, 1960) and embryology of *Eremitalpa* (Broom, 1943; Gabie, 1959; Van der Horst, 1946) show that the early development of the species conforms with that of other eutherian mammals, although certain features are primitive.

DISTRIBUTION AND GENERAL ECOLOGY

The distribution of *E. granti* extends from St. Helena Bay in the western Cape Province, northwards to Walvis Bay in Namibia (Smithers, 1983). *Eremitalpa. g. granti* is found south of the Orange River from St. Helena Bay to Port Nolloth (Meester *et al*., 1986; Roberts 1951), while *E.g. namibensis* occurs north of the Orange River in the Namib Desert in the sand dune areas south of the Kuiseb River (Coetzee, 1969; Meester *et al*., 1986; Stuart, 1975) (Fig. 1.2).

Earliest collections of *E.g.namibensis* were from owl pellet remains at Sossusvlei (Bauer & Niethammer, 1959) and Natab (Meester, 1962), while Haake (1963) captured the first live specimen near Gobabeb.

Eremitalpa g. namibensis is confined to sand dunes and is particularly abundant on the well vegetated dune plinth (Coetzee, 1969; Holm & Scholtz, 1980; Robinson & Seely, 1980), although Holm (1969) also recorded *E.g. namibensis* in the sandy river bed of the Kuiseb River near to Gobabeb. No evidence of permanent tunnel systems or burrow chambers has been found. *Eremitalpa g. namibensis* moves just below the surface of the sand leaving ridges of sand, or else locomotion is totally emerged on the surface (Coetzee, 1969; Holm, 1969). Nocturnally active (Holm, 1969), their skulls and bones are common items in the casts of owls (Nel, 1969; Skinner, Lindeque, Van Aarde & Dieckmann, 1980; Tilson & Le Roux, 1983). Gut content analysis on three moles from the Kuiseb River bed revealed termites, ants, mealybugs (Pseudococcidae) and tenebrionid larvae as natural food items (Holm, 1969). Virtually nothing is known about the reproductive biology. Two gravid females caught near Gobabeb (Holm, 1969) were each found with only one almost fully developed embryo, indicating small litter sizes.

No external parasites were found on animals caught during this study. Internally, Acanthocephalan cystacanths (Family

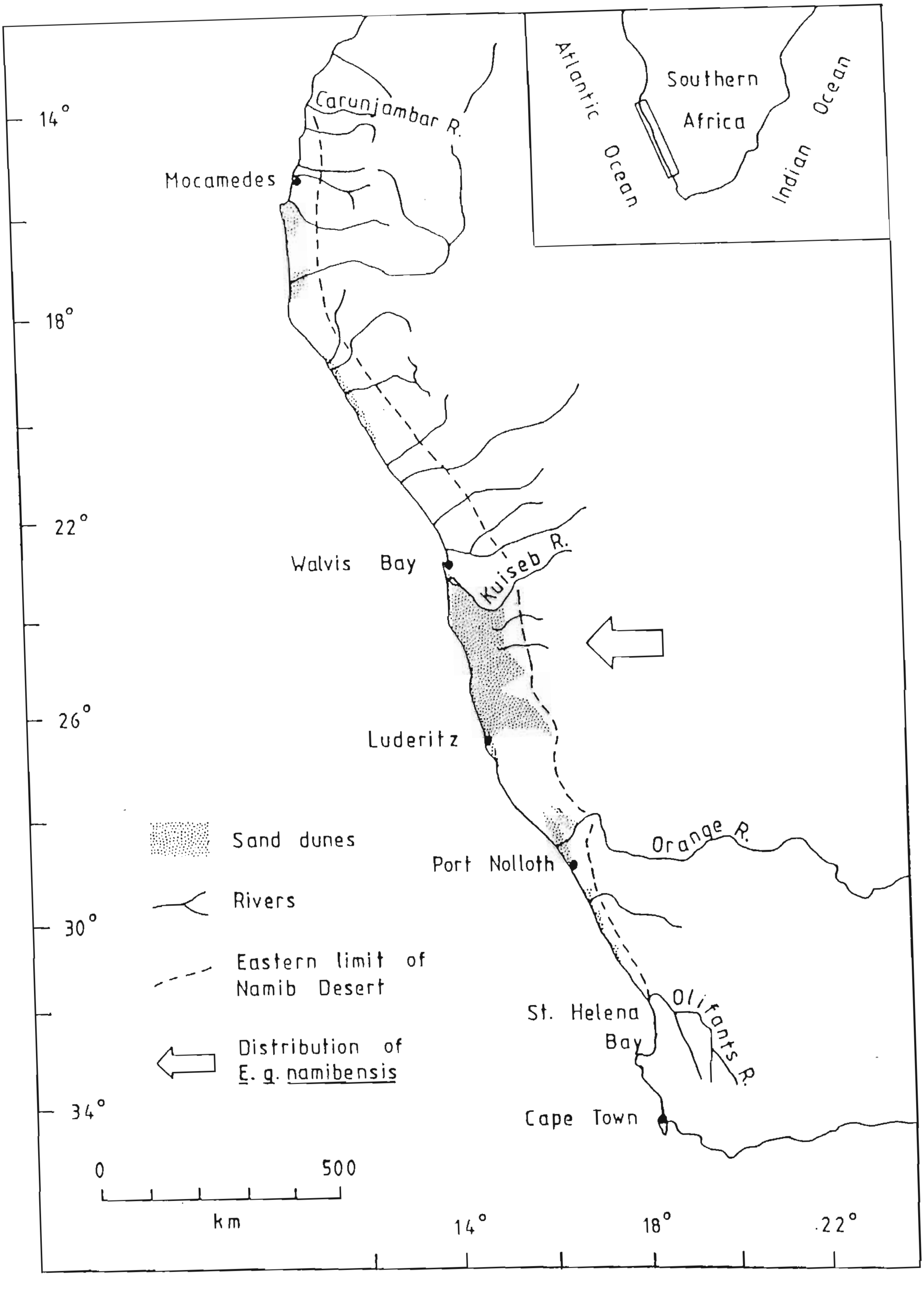


FIGURE 1.2: The Namib Desert with distributional range of E.g. namibensis indicated. Modified from Ward et al. (1983).

Oligacanthorynchidae) were isolated from the peritoneal cavity (Spencer-Jones, *in litt.*).

STUDY AREA

The Namib Desert forms a coastal strip, mostly less than 200km wide, and extending some 2000km along the south western coast of Africa, from approximately the Olifants River (Cape Province, South Africa) to the Carunjamba River (Mocamedes district, Angola) (Goudie, 1972). Within this area lie several sand dune masses of which the main dune area, the southern dune field, extends 400km south of the Kuiseb River to Luderitz (Ward, Seely & Lancaster, 1983) (Fig. 1.2).

The main study area was selected within the southern dune system in the vicinity of Gobabeb (23° 34'S, 15° 03'E) on the northern margin of the dune mass, 60km from the coast (Fig. 1.3). The dune site therefore borders on two other desert habitats within the central Namib, namely the riverine habitat supported by subterranean water beneath the dry Kuiseb River bed, and the flat gravel plains to the north of the river. The study area was chosen because of its proximity to the research station (The Desert Ecological Research Unit) at Gobabeb. A secondary study area was situated at Far East (23° 45'S, 15° 30'E) on the eastern edge of the southern dune sea 130km from the coast (Fig. 1.3). Because of difficulty with transport, only limited field observations (concerning feeding biology and foraging behaviour) were conducted in this area.

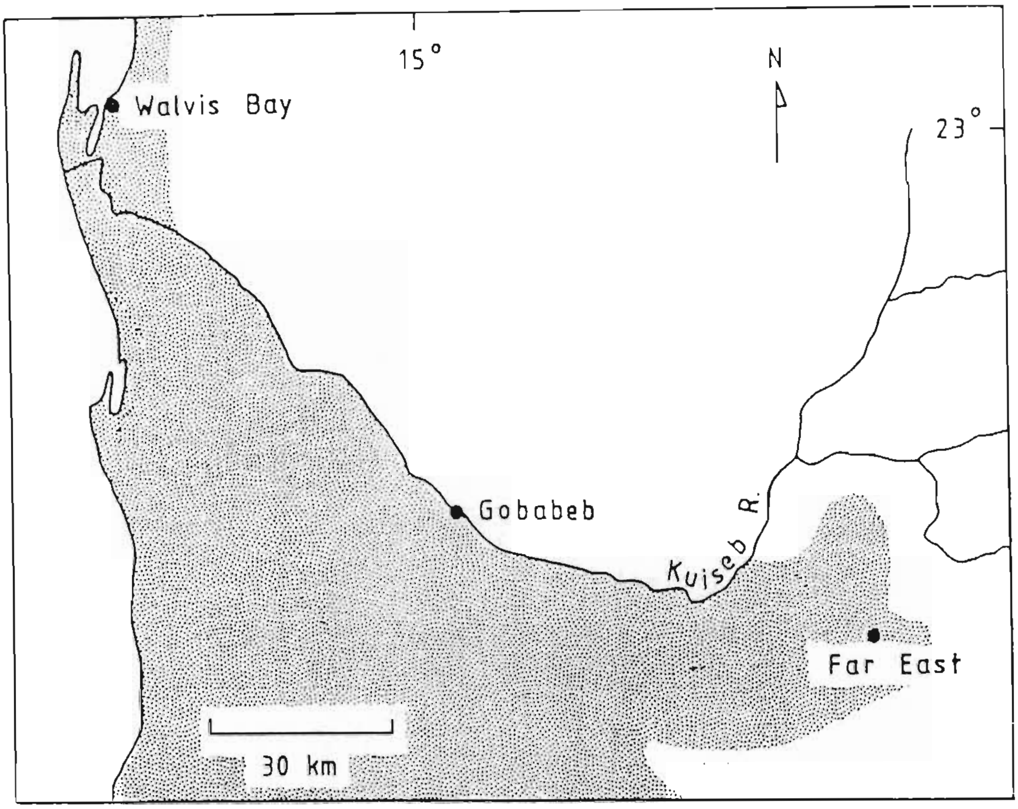


FIGURE 1.3: The southern dunes (shaded) of the Namib Desert showing position of two study areas.

Climate

The Namib is a cool coastal desert with a mild warm temperate to subtropical climate and no strong seasonal climatic changes (Schulze & McGee, 1978). Nevertheless, climatic gradients change rapidly from the coast to the eastern edge of the dune field, to the extent that three macroclimates have been defined (McClain, Seely, Hadley & Gray, 1985). These are cool, foggy desert on the coast, alternating fog desert in the interior (Gobabeb) and warm inland desert on the eastern edge of the dune field (Far East). Detailed macro-meteorological information for the three climatic zones are given in Lancaster, Lancaster and Seely (1984), Schulze (1969) and Seely and Stuart (1976). Data pertinent to Far East and Gobabeb are summarised in Table 1.2. Both areas are characterised by marked diurnal ranges of temperature and humidity and low precipitation. At Gobabeb precipitating advective fogs are present an average of 36 days per year, and have been recorded for every month (Besler, 1972). At Far East, fog occurrence is extremely rare with nearly all of the annual precipitation occurring as discrete rainfall events during the summer months of December to April.

Dune Topography and Vegetation

The southern Namib dune system can be divided into various habitats based on dune topography and the distribution of the biota. The following broad classification has frequently been employed (Holm & Scholtz, 1980; Robinson & Seely, 1980; Seely & Louw, 1980) (Fig. 1.4):

TABLE 1.2: Meteorological data from Lancaster *et al.* (1984) obtained from weather stations near to the study sites or on a similar longitude. Values represent yearly averages based upon mean monthly values over a 5-18 year period.

	Gobabeb	Far East
Temperature (^{o}C)		
Maximum	29.5	28.5
Minimum	12.8	14.6
Mean	21.1	21.5
Relative humidity (%)		
Maximum	75	58
Minimum	24	19
Mean	50	37
Precipitation (mm)		
Fog	30.8	2.7
Rain	27.2	87.0
Total	58.0	89.7

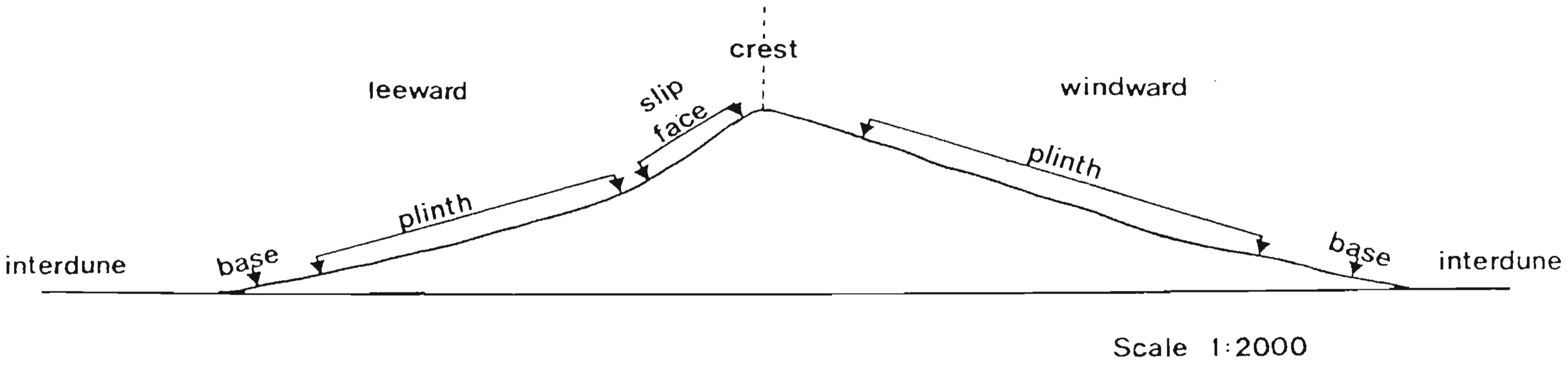


FIGURE 1.4: Topographically and ecologically distinct regions of a linear dune. Modified from Robinson and Seely (1980).

1. The interdune valleys
2. The vegetated lower portion of the dune consisting of the dune base and plinth
3. The vegetationless dune crest system.

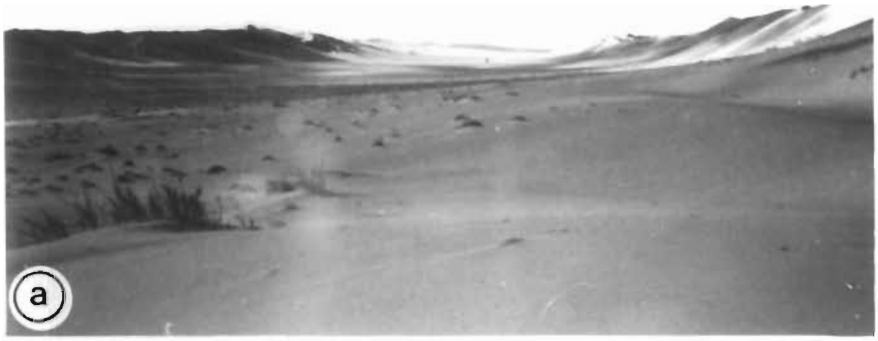
At Gobabeb (Plate 1.2a), the interdune valleys are stony and only occasionally covered by sand, with the average width being 1.8km. Average height of the dunes is 80-100m (Goudie, 1972). At Far East (Plate 1.2b), although the basic linear dune format is still evident, the dune ridges tend to be a chain of interconnnected multifaceted star dunes (Lancaster, 1983) usually less than 30m high with interdune valleys about 2km wide (Boyer, 1987).

Detailed descriptions of the vegetation of the dunes and interdune valleys of the southern dune system, including the study areas can be found in Boyer (1987), Holm and Scholtz (1980), Robinson (1976), Robinson and Seely (1980), Seely and Louw (1980) and Yeaton (1988).

The following synopsis is compiled from Robinson and Seely (1980).

At Gobabeb, the flat interdune valleys are usually devoid of vegetation since soil is shallow and moisture storage brief. On the dune slopes, soil moisture and sand stability are generally greatest in the lower strata. Consequently, the perennial flora exists almost entirely on the dune base and plinth communities. Plants characteristic of the dune base

PLATE 1.2: Characteristics of dune field at Gobabeb (a) and Far East (b).


a


b

are grasses (*Asthenatherum glaucum* and *Caldoraphia spinosa*), a leaf succulent (*Trianthema hereroensis*) and the Nara melon (*Acanthosicyos horrida*). On the plinth, the dune endemic grass *Stipagrostis sabulicola*, is often co-dominant with *T. hereroensis*. These two species often form large hummocks 1-2m high. From the dune base, plant coverage decreases upslope and is usually entirely absent in the upper third of the plinth and the dune crest and slipface regions. In these areas, plants cannot germinate or become established due to winds producing a highly mobile substrate. Instead 'primary production' is in the form of wind-blown organic detritus which accumulates on the sand surface.

At Far East, where the dominant moisture source is rain, vegetation communities are more complex and diverse (Boyer, 1987; Yeaton, 1988). Dense monospecific stands of *S. ciliata* cover the interdune valleys while the dune slope is densely vegetated with several species of perennial grasses including *C. spinosa*, *S. sabulicola*, *S. lutescens*, *S. ciliata* and the shrub *Kohautia ramosissima*. The dune crest region is more compacted and stable than at Gobabeb and is dominated by *C. spinosa* and *S. sabulicola*.

Fauna

The fauna of the southern dune system is typically deserticolous and is composed almost entirely of insects, arachnids and reptiles (Holm & Scholtz, 1980; Kock, 1953, 1961, 1962; Lawrence, 1959; Robinson & Seely, 1980; Seely, de Vos & Louw, 1978).

Comprehensive checklists of mammals occurring in several distinct habitat types within the Namib Desert are given in Coetzee (1969) and Stuart (1975). Of the 80 species listed, relatively few occupy the sand dune habitats typical of the two study areas and include the Namib golden mole, two species of gerbils, (*Gerbillurus paeba* and *G. tytonis*) and the Cape hare (*Lepus capensis*). Several carnivore predators, i.e. Cape fox (*Vulpes chama*), genet (*Genetta genetta*) jackal (*Canis mesomelis*) and spotted hyaena (*Crocuta crocuta*) are resident in the riverine growth of the dry Kuiseb River and may, on occasion, enter the dune areas (Stuart, 1975). Of the large ungulates, only the gemsbok (*Oryx gazella*) enters the dune system for long periods when food is abundant (Seely & Louw, 1980).

Avian raptors which roost in the riverine growth of the Kuiseb, but hunt over the dunes at night, include the barn owl (*Tyto alba*) and the spotted eagle owl (*Bubo africanus*) (Tilson & Le Roux, 1983). Crows (*Corvus alba*) and pale chanting goshawks (*Melierax canorus*) were sometimes seen in the dunes near Gobabeb during the day.

MATERIALS AND METHODS

Capture

Surface locomotion in *E.g. namibensis* results in formation of clearly defined trails along the dune surface. The most simple way of catching moles, was to follow surface trails to their termination, and then dig rapidly by hand down into the sand to retrieve the animal, usually at a depth not greater than 20cms. Tracking was usually done between sunrise and 10h00 since later in the day, wind action and dune surface glare made it difficult to locate surface trails.

If capture by digging proved unsuccessful, an enclosure of pit-fall traps and drift fences was constructed around the excavation site (Plate 1.3). Enclosure size varied (3-10m diameter) and was usually determined by the size of the plant hummock beneath which the mole was buried. Drift fences were constructed of corrugated-iron sheets of variable length (0.5-2.0m) and uniform width (0.8m) hammered into the sand with a rubber mallet, to a depth of approximately 0.3m. Separating adjacent metal sheets were small plastic buckets (width 15cm, depth 15cm) buried so that the bucket rim lay flush with the sand surface and was in contact with the edge of the drift fence. Sand to a depth of 5-8cm was placed in the bottom of each bucket to allow moles to burrow.

The principle of capture was simple. After emergence onto the sand, moles soon came into contact with a section of drift fence submerged at a depth sufficient to discourage attempts to burrow beneath it. Unable to escape by digging, moles attempted to travel around the obstacle, and in so doing, were inadvertently guided into a plastic pit-fall trap. Traps were set in late afternoon before the nocturnal activity

PLATE 1.3: Pit-fall trap and drift fence enclosure.

periods, and left undisturbed before checking the following morning.

Table 1.3, shows the results of a trapping survey conducted at Gobabeb in March 1987. Moles buried beneath clumps of vegetation were far more difficult to retrieve than those buried in open sand, since presence of plant roots and spinacious foliage hindered digging efforts. Overall a 21% success rate was achieved using the follow-and-dig method. Capture success, using pit-fall traps, was considerably greater than by the follow-and-dig method (81%). Failure of the pit-fall method resulted primarily from small gaps left between the rim of the plastic bucket and adjacent sheets of drift fence which allowed moles to escape. On one occasion, strong winds during the night resulted in the plastic buckets filling up with sand, hence rendering the traps ineffective.

In spite of its effectiveness, pit-fall trapping was seldom used during the course of this study, since construction of enclosures was extremely labour intensive, and transport of trap materials impractical.

Keeping Moles in Captivity

All laboratory studies involving water metabolism, thermoregulation and activity phasing were conducted in the Department of Zoology and Entomology, University of Natal, Pietermaritzburg.

Animals used in these studies were caught by hand or by pit-

TABLE 1.3: Capture success of E.g. namibensis over a five day period at Gobabeb, March 1987.

Method	Trails followed	Termination of trail	Moles caught	Capture success
Follow-and-dig	29	vegetation clump	3	10.3%
	4	open sand	4	100.0%
Total	33		7	21.2%
Pit-fall trap and drift fence	21	vegetation clump	17	81.0%

fall trap in the Namib sand dunes at Gobabeb, and airfreighted to the laboratory facilities at the University of Natal. Moles were maintained individually in 60 x 30 x 30cm glass terraria in a windowless room at 25°C and ambient humidity with a 12 hour photoperiod (fluorescent lights from 07h00 - 19h00). Each animal was provided with Namib dune sand (10-15cm depth) and a heat source in the form of a desk lamp equipped with a 50w incandescent red light bulb in one corner of the terrarium. Moles were fed daily with mealworm larvae (*Tenebrio molitor*) and on occasion (every two to three weeks), one-day old mice (*Mus musculus*). Water in a shallow petri dish was initially provided, but subsequently removed, since moles were not observed to drink. Sand was kept clean by sieving every two weeks to remove excretory residues. Animals maintained under these conditions survived six months to three years in captivity.

Statistical Methods

Zar (1974) was used as the standard reference for all statistical tests used in this thesis.

CHAPTER 2

FEEDING ECOLOGY AND FORAGING BEHAVIOUR[1]

INTRODUCTION

The extensive underground burrow systems constructed by subterranean mammals provides a sheltered environment, escape from surface predators and access to food. However, these advantages are gained at the expense of the high energy cost of burrowing. Vleck (1979) found that for the pocket gopher (*Thomomys bottae*) burrowing is 360 to 3400 times more energetically expensive than moving the same distance across the surface. It follows that in subterranean mammals, adaptations to reduce the cost of foraging, or alternatively, to increase foraging efficiency, will be under relatively intense selection pressure (Anderson, 1982; Du Toit, Jarvis & Louw, 1985; Jensen, 1986), especially in desert environments where productivity is extremely low (Louw & Seely, 1982).

E. g. namibensis, does not inhabit permanent burrow systems, but instead spends the daylight hours buried in soft dune sand. Unlike the majority of subterranean insectivores, the Namib mole is a surface forager and hunts prey on the dune surface at night. Such divergence from the typical subterranean mode is obviously partly as a result of

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[1] This chapter together with abstract, acknowledgements and references is *in press* in the *Journal of Zoology (London)* under the full title 'Feeding ecology and foraging behaviour of the Namib Desert golden mole *Eremitalpa granti namibensis* (Chrysochloridae)' and is co-authored with M.R. Perrin and G.C. Hickman.

the environmental constraint of constructing large complex burrow systems in soft shifting dune sand. However, adaptations to reduce the cost of foraging must also play an important role.

To understand the adaptiveness of an animal's foraging behaviour requires a knowledge of prey selection (the choice by the animal of which foods to eat), distribution of prey in the environment and finally the movement patterns of the predator in relation to resource distribution (Krebs, Housten & Charnov, 1981; Pyke, 1984; Pyke, Pulliam & Charnov, 1977).

To elucidate the adaptive response of E. g. namibensis to its' desert environment, the following items were considered:

1. Natural diet and food preferences.
2. Resource abundance and distribution in the natural habitat, the Namib dunes.
3. Qualitative and quantitative description of searching behaviour.
4. Movement patterns of E. g. namibensis with regards to the distribution and variation in prey resources.

MATERIALS AND METHODS

Study Sites

The two study areas were at Gobabeb and at Far East. These two sites differ in vegetation density and species diversity, with the most diverse and dense coverage occurring at Far East.

Stomach Content Analysis

Nineteen moles were captured by hand (16 from Gobabeb, three from Far East) from December of 1983 to October of 1984. All moles were adults (nine males, ten females). Catching of moles at regular intervals throughout the year proved impracticable, thus no attempt was made to examine seasonal variation in diet composition.

Animals were taken to the laboratory as soon as possible after capture and sacrificed with chloroform. Stomach contents were prepared using the methods of Funmilayo (1979) and Korschgen (1971). Stomachs were removed, put into 4% formalin for 24 hours to harden the contents, rinsed in water and dried on filter paper. Contents were removed and stored in 70% ethanol until examination.

Stomach contents were placed in a petri dish and examined under a binocular microscope (6x magnification). A reference collection of the most abundant sand dwelling invertebrates in the Gobabeb and Far East vicinities was used to identify items down to ordinal level.

Food habits were expressed as follows:

1. Frequency of occurrence: derived from the number of stomachs in which a particular food item occurred.
2. Percentage volume (Kruuk & Mills, 1983): whereby the percentage volume of each order of prey item in individual stomachs was estimated by eye. The final estimate was calculated as an average of all estimates

for individual samples. The two above methods were used since a single criterion is often inadequate to provide meaningful results (Korshgen, 1971; Kruuk & Parish, 1981). For example, a single food item identified in a sample receives the same frequency rating as a full stomach of the one item. High frequency together with high volume, indicate a food of high preference.

3. Enumeration: numbers of items in each order of prey item occurring in each stomach were totalled. These data were used for comparison of dietary composition with that of resource availability in the field (Feinsinger & Spears, 1981).

Laboratory Observations

Observations on feeding behaviour were made on captive animals. No food preference tests were conducted, but a large variety of different prey items was offered so that some indication of dietary range was obtained.

Determination of Prey Availability

Prey availability at Gobabeb was assessed by sampling the sand dwelling fauna of the dune slope and that associated with the three dominant plant species, a woody dune succulent (_Trianthema hereroensis_), and two perennial grasses (_Stipagrostis sabulicola_ and _Cladoraphia spinosa_).

Plants were selected at random and an area $0.25m^2$ cleared of surface vegetation. Within the confines of this cleared area, sand was excavated to a depth no greater than that to which moles may submerge while foraging (approximately 0.15m). Excavated sand was sieved using a mesh size of $0.04cm^2$. All animals collected from sieving were taken back to the laboratory for identification and processing. For each plant excavated, presence or absence of termite casts (hollow cylindrical structures of solidified sand with an inside diameter of approximately 2-3mm) was noted. Ten series of 60 samples (20 for each plant species) were taken at intervals of one month from August 1983 to July 1984. To ensure that items collected were representative of those encountered by moles during their nocturnal foraging period, all sampling was conducted after sunset. In addition to plant excavation, 100 randomly chosen sites on the dune slope where no vegetation was present were excavated in a similar fashion to that described above.

Animals extracted from samples by sieving were identified (to at least order), counted and weighed. After drying to constant mass at $60^{\circ}C$, items were reweighed and water content determined by subtraction of dry mass from wet mass. Mass of invertebrates was expressed as g dry mass m^{-2}.

To test for differences in prey availability between Gobabeb and Far East, excavation samples were taken from a plant species abundant in both areas, _S_. _sabulicola_. Twenty plants from each area were sampled during September 1984. Mass of excavated invertebrates was again expressed as g dry mass m^{-2}.

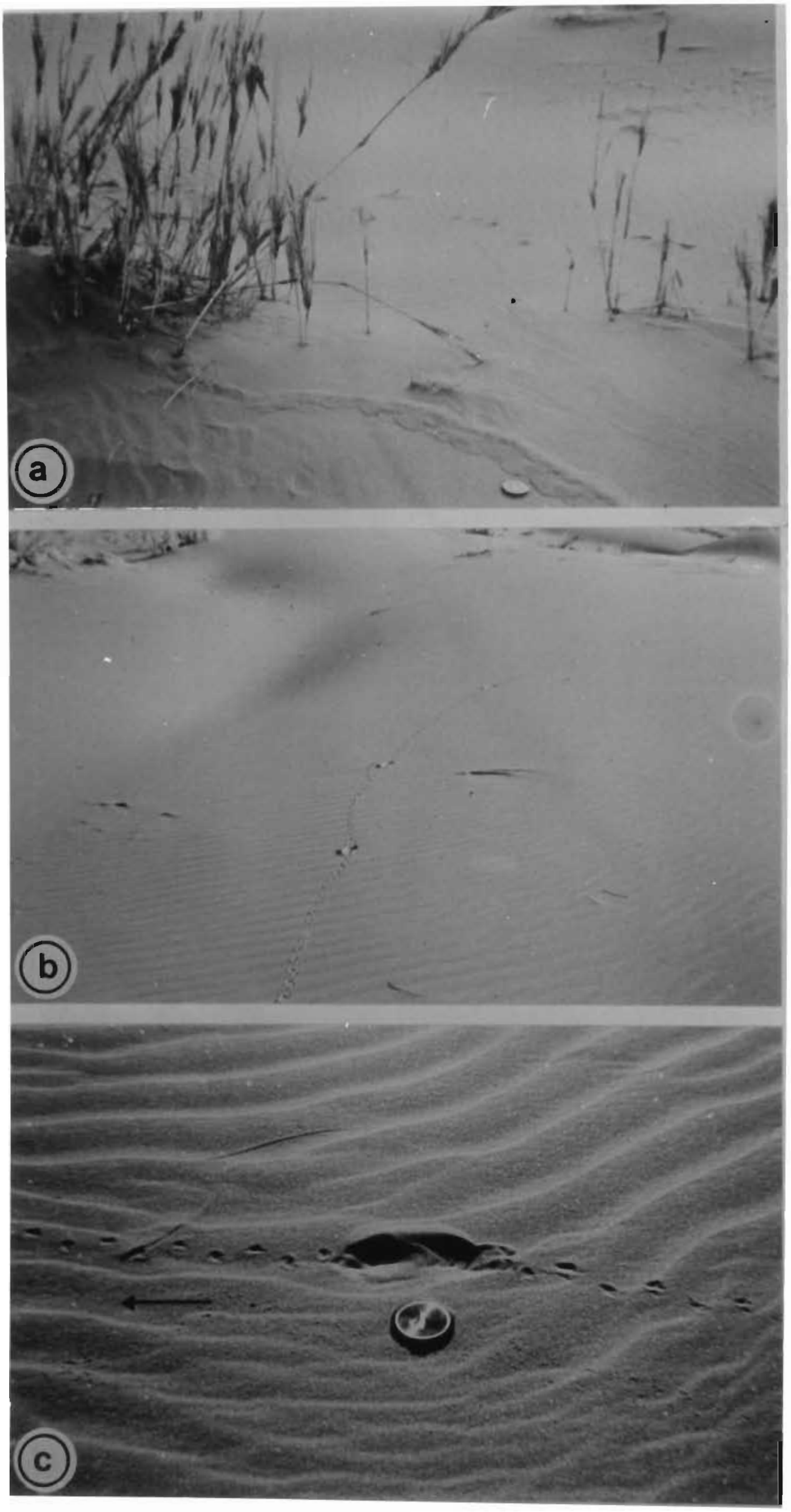
Mapping Foraging Paths

Moles active in the sand dunes during their nocturnal foraging period leave a clear record of their movement patterns on the dune surface (Plate 2.1). Tracks made by moles moving just below the sand surface are shown in Plate 2.1a. This behaviour, termed sandswimming by Coineau (1981) and Holm (1969), and described in considerable detail by Gasc, Jouffroy and Renous (1985) does not result in surface mounds characteristic of subterranean mammals (Hickman, 1985). Instead, a characteristic ridge is formed by the sand collapsing in on the wake of the passage of the mole through the sand. More often, moles move on the sand surface (Plate 2.1b). A typical path consists of a length of surface tracks punctuated by 'dips' or 'furrows' marking the point where the mole has briefly submerged into the sand (Plate 2.1c). The important feature of this locomotory pattern is that the movement of moles is conveniently divided into a series of natural units comprising the successive moves and the turns made between them.

A series of mole tracks were mapped in areas of low (Gobabeb) and high (Far East) vegetation densities during 1983 and 1984.

The variables measured for the foraging paths of the moles are listed below and are illustrated in Fig. 2.1.

1. Total length of the foraging pathway.
2. Proportion of surface to subsurface movement.
3. Distance moved between dips.


a
b
c

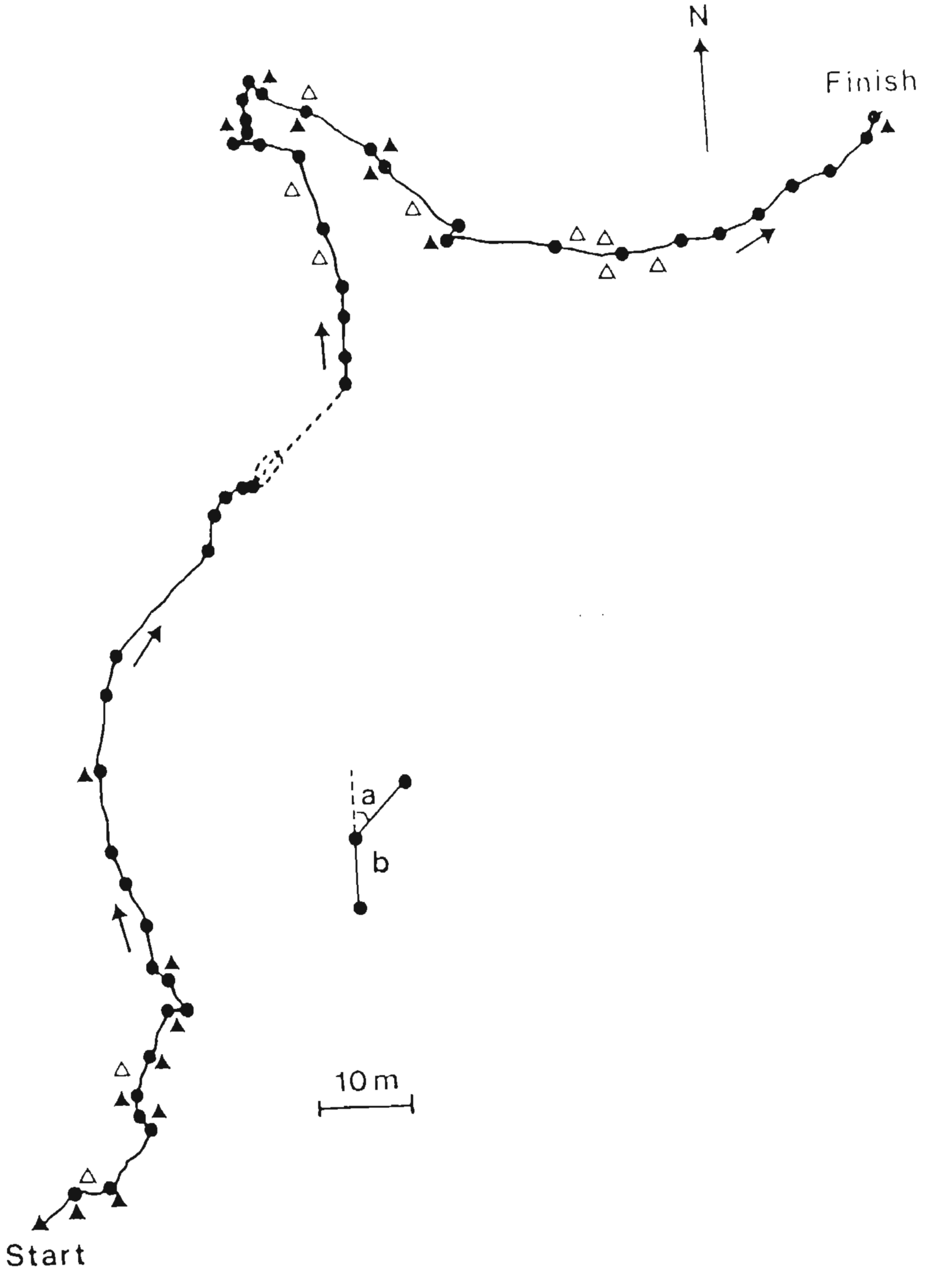


FIGURE 2.1: Section of foraging path of E.g. namibensis mapped at Gobabeb. Solid and broken lines indicate surface and subsurface movement respectively, solid circles represent foraging dips, solid triangles are plants encountered along track, open triangles are plants bypassed within 1m of track, a is angle of turn between successive moves, b is move distance between dips.

4. Angles of turn between successive moves relative to the direction of the preceding move. These angles were assigned either to right or left depending on the turn.
5. Number of plants encountered along the length of a foraging path.
6. Foraging intensity at each plant clump encountered. Foraging intensity was measured as the distance of subsurface movement (m) around the base of the plant. This subsurface movement consisted either of one or more dips or else a continuous stretch of sandswimming.

RESULTS

Dietary Composition

The three stomachs examined from the Far East area showed no marked differences in diet composition to those in the Gobabeb area. Thus Fig. 2.2 gives the percentage volume of prey items together with frequency of occurrence in the diet for the two areas combined.

E. g. namibensis consumed a wide variety of predominantly sand dwelling invertebrates. Isopterans (Psammotermes allocercus silvestri) were the major dietary item constituting both the highest volume and frequency of occurrence. Coleopteran larvae were the second most important food item. The remaining dietary components included insect larvae, Araneida, Thysanura, Formicidae, Coleoptera and Skincidae which were taken infrequently with each contributing less than 5% of the total volume. Plant roots may have been incidentally

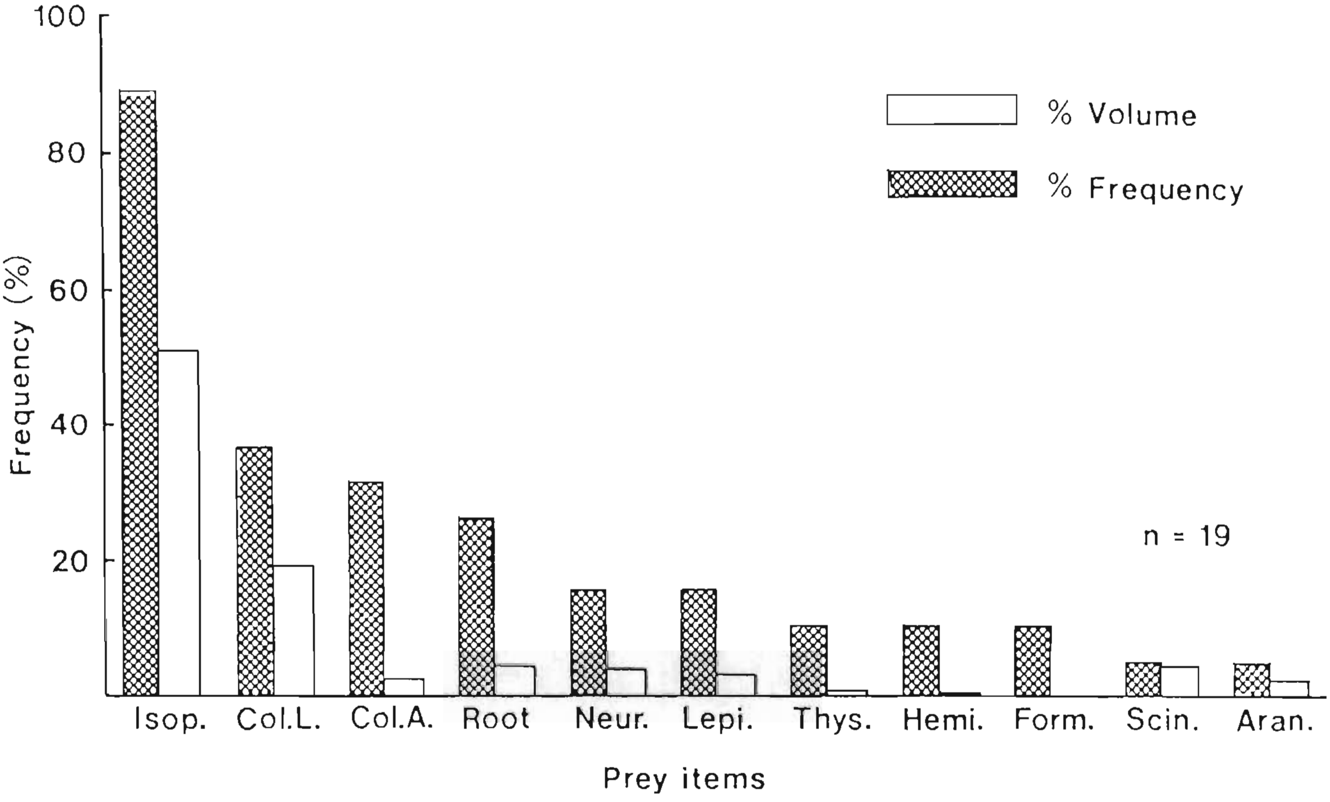


FIGURE 2.2: Dietary composition of E.g. namibensis in the Namib dunes at Gobabeb and Far East. From left to right, abbreviations for Isoptera, coleopteran larvae, coleopteran adults, root material, neuropteran larvae, lepidopteran larvae, Thysanura, Hemiptera, Formicidae, Scincidae and Araneida.

ingested. All stomachs contained traces of sand as a consequence of prey being devoured below the sand surface.

Prey Availability

The relative availability of invertebrates obtained from dune slope and plant excavation at Gobabeb is presented in Fig. 2.3. The results are expressed as g dry mass m^{-2} since the mass of a population of a prey item is a better indication of its food potential than are its numbers. Because of the highly variable nature of the data, the median biomass was considered to be a more meaningful statistic than the mean. No significant differences were found between arthropod biomass in the three plant species at Gobabeb (Kruskal-Wallice H test: H=3.92; p>0.10; d.f.=2). In comparison, the mass of invertebrates from the dune slope was negligible with a median biomass of zero.

The occurrence of termite workings was also considerably greater under plants than on the dune slope. No significant differences in cast abundance were found between the three plant species (chi-square test: χ^2= 4.1; p>0.05; d.f.=2), with the mean frequency of occurrence being 76% as opposed to 9% for the dune slope.

Differences in arthropod biomass between S. sabulicola plants at Gobabeb and Far East (Fig. 2.4) were not significant (Mann-Whitney U test: U=241; p>0.20; d.f.=20,20). Frequency of occurrence of termite casts in S. sabulicola compared favourably for both areas being 85% and 75% for Gobabeb and

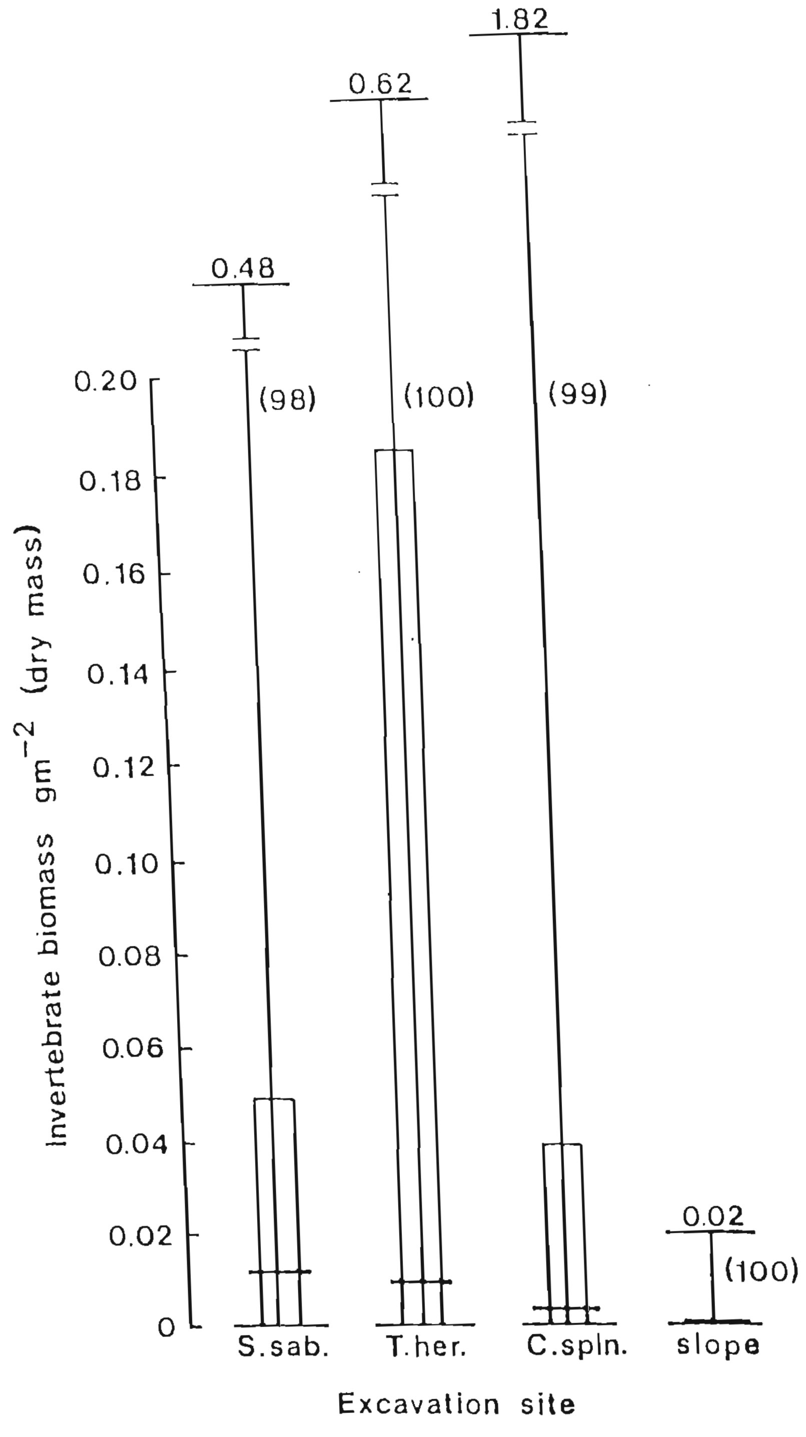


FIGURE 2.3: Invertebrate biomass excavated from dune slope and dune plants at Gobabeb. Horizontal bars indicate median values, boxes enclose lower and upper quartiles, vertical lines indicate range of values, numbers in parentheses give sample size.

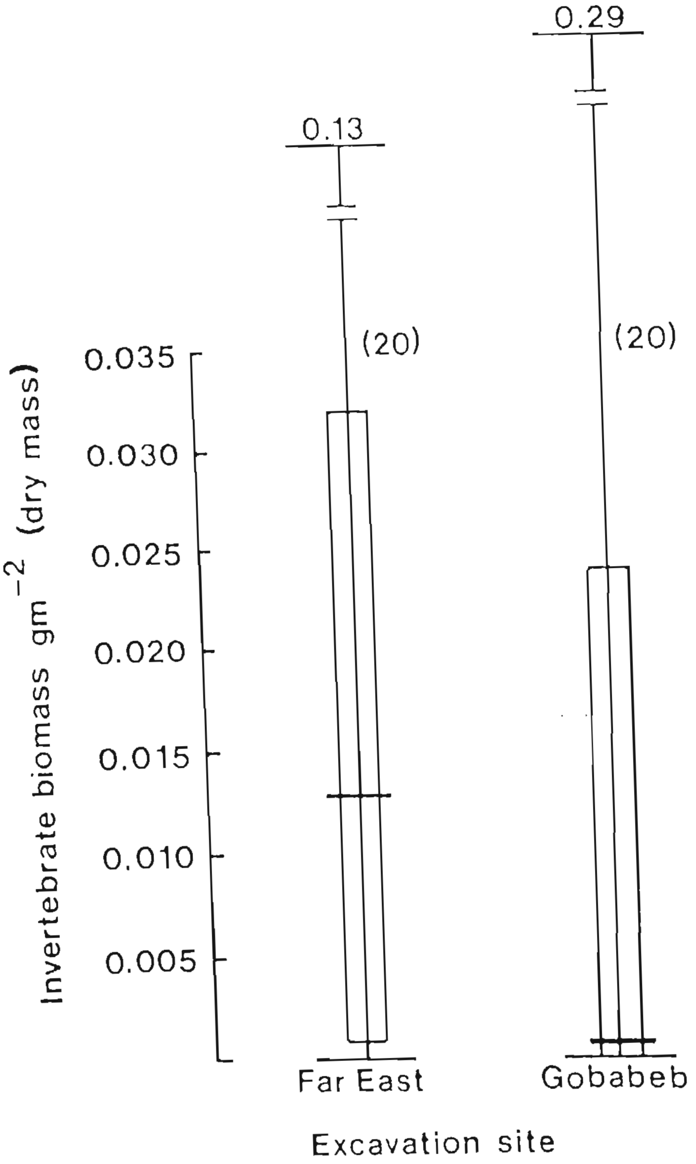


FIGURE 2.4: Invertebrate biomass excavated from *S. sabulicola* at Gobabeb and Far East. Horizontal bars indicate median values, boxes enclose lower and upper quartiles, vertical lines indicate range of values, numbers in parentheses give sample size.

Far East respectively.

Natural Food Preferences

To assess the natural food preferences of E. g. namibensis, prey availability in the field was compared with the diet composition of the moles. Since only three animals were procured from Far East, it was considered prudent to restrict the assessment to the 16 moles captured in the Gobabeb vicinity.

Numerical abundance of prey items in the field compared to that in the diet are given in Table 2.1. With regard to relative abundance of isopterans, coleopterans and thysanurans, there was a marked difference between diet composition and prey availability. Termites, although constituting a major component of the diet, were seldom found in the field, whereas coleopterans and thysanurans, which together comprise less than 0.5% of the diet by number, were very common. Since several items were represented by low numbers in the field and not at all in the diet, their absence from stomach contents was likely a reflection of the small sample size of stomachs examined rather than rejection as a food source. No vertebrate taxa were collected in the field, although lizards and snakes were present in the study area.

Water Content of Prey Items

Water content of some of the more numerous taxa of arthropods recovered from plant excavation are given in Table 2.2. All groups tested differed significantly from each other with

TABLE 2.1: Dietary composition of E. g. namibensis in comparison to prey availability at Gobabeb.

	Percentage composition by number	
Item	Diet (n=16)[a]	Field (n=397)[b]
Isoptera	97.5	0.2
Insect larvae	1.7	9.4
Coleoptera	0.3	27.7
Formicidae	0.2	0.0
Araneida	0.1	5.5
Thysanura	0.1	50.1
Hemiptera	0.1	0.2
Scincidae	0.1	0.0
Hymenoptera	0.0	1.2
Mantidae	0.0	0.5
Solpugida	0.0	0.2
Total items	2133	415

[a] Number of stomachs examined

[b] Number of excavation samples

TABLE 2.2: Water content of prey items recovered from excavation sampling. Also listed are results of one way analysis of variance and statistical probabilities for significant group mean comparisons determined using Student-Newman-Keuls multiple range test.

	Taxa	n	Mean water content ± 1 S.D. (gg^{-1} wet body mass)
1	Coleoptera	38	0.50 ± 0.12
2	Thysanura	26	0.59 ± 0.08
3	Insect larvae	27	0.68 ± 0.11

F = 21.58; $p<0.001$; d.f.=2,88

1 < 3; $p<0.001$

1 < 2; $p<0.001$

2 < 3; $p<0.001$

adult Coleoptera having the lowest water content and insect larvae the highest.

Laboratory Observations of Feeding Behaviour

Prospective food items offered to captive moles included lizards (*Aporosaura anchietae*), geckos (*Palmatogecko rangei*), legless lizards (*Typhlosaurus braini*), tenebrionid beetles (*Onymachris* species), crickets, a variety of insect larvae and pupae, spiders, harvester termites, grasshoppers and one day old mice (*Mus musculus*) as well as small lumps of raw minced beef.

The above items were placed onto the surface of the sand in the terrarium where their movements attracted the attention of the moles. Motionless objects such as minced meat and insect pupae were ignored. The moles moved towards the source of movement just below the sand surface. Occasionally only the head and nose surfaced to 'sniff' the air briefly before submerging again. Prey items such as insect larvae and termites were seized from beneath and dragged down into the sand to be consumed. In some instances the moles, on encountering a prey item, would surface, seize the prey in the mouth and front claws and then proceed to push rather than pull the item down into the sand. This behaviour was observed many times with infant mice. In pursuing active prey such as lizards, geckos, beetles, crickets and grasshoppers, moles ran rapidly along the sand surface, occasionally briefly submerging their head and shoulders, possibly in an attempt to detect the position of the prey from substrate vibrations. Tenebrionid beetles were often caught, but not consumed because of the inability of the moles to bite through the hard exoskeleton. If the exoskeleton was cracked open prior to introduction into the terrarium, the soft inner organs of the beetle were readily consumed, although the hard chitinous parts of the head, thorax and abdomen were left untouched. Successful catching of lizards, geckos, crickets and grasshoppers was never observed in the laboratory. On one occasion in the field, it was apparent from the pattern of tracks on the dune surface that a mole had come across and consumed a lizard.

Patterns of Movement

The length of foraging tracks measured at Gobabeb and Far East are shown in Fig. 2.5. There were marked differences in path length between the two areas. Some tracks at Gobabeb extended to over 550m in length, whereas at Far East 200m was the maximum, with most of the tracks measuring less than 50m.

The proportions of surface to subsurface movement also differed between the two sites (Fig. 2.6). At Gobabeb, the tracks were nearly entirely on the surface with only a few having more than 25% of their length subsurface. Sandswimming was found in three types of situations.

1. For 1-2m at the beginning and/or end of the foraging track where the mole had either submerged or emerged from its daytime refuge.

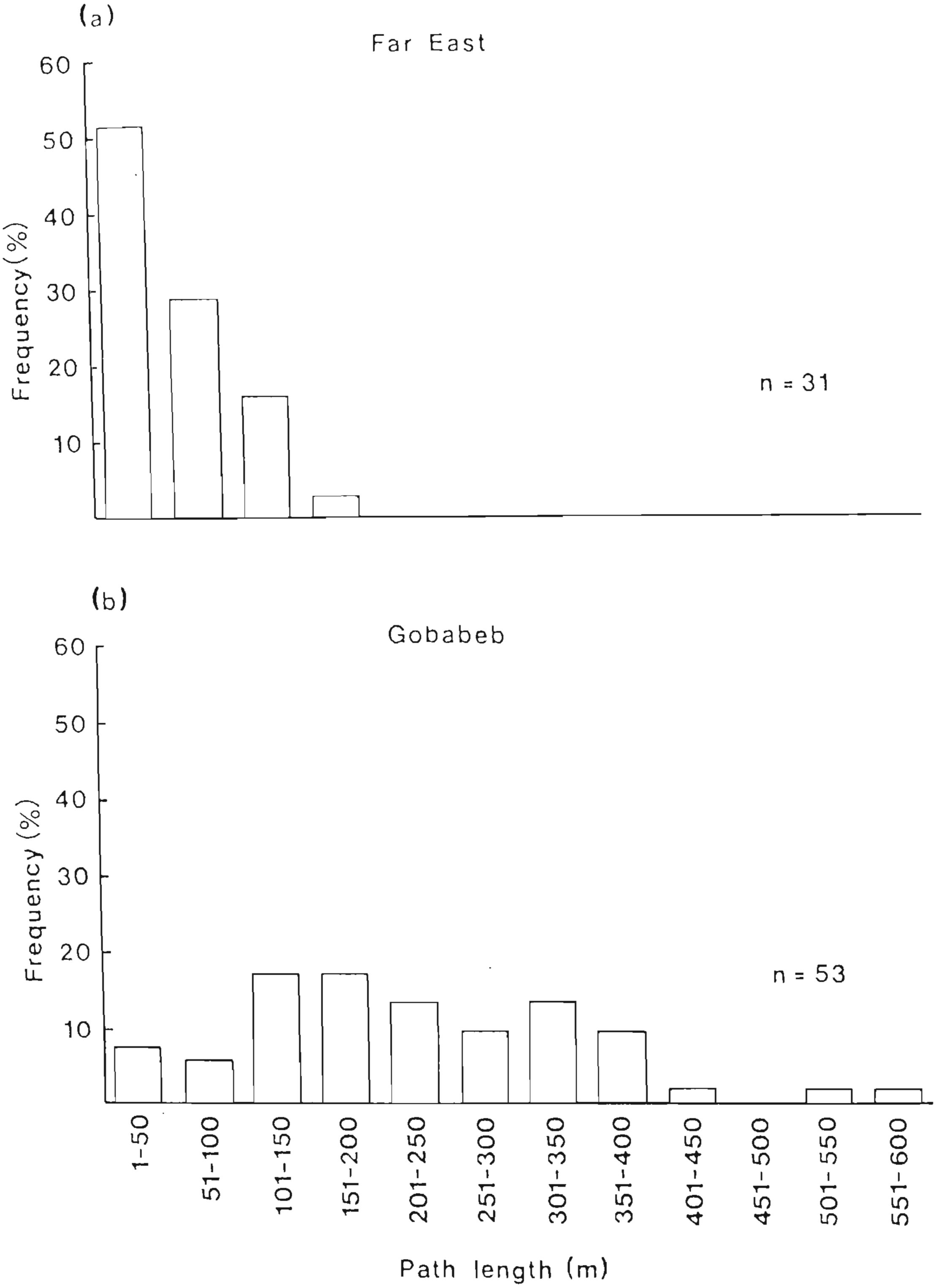
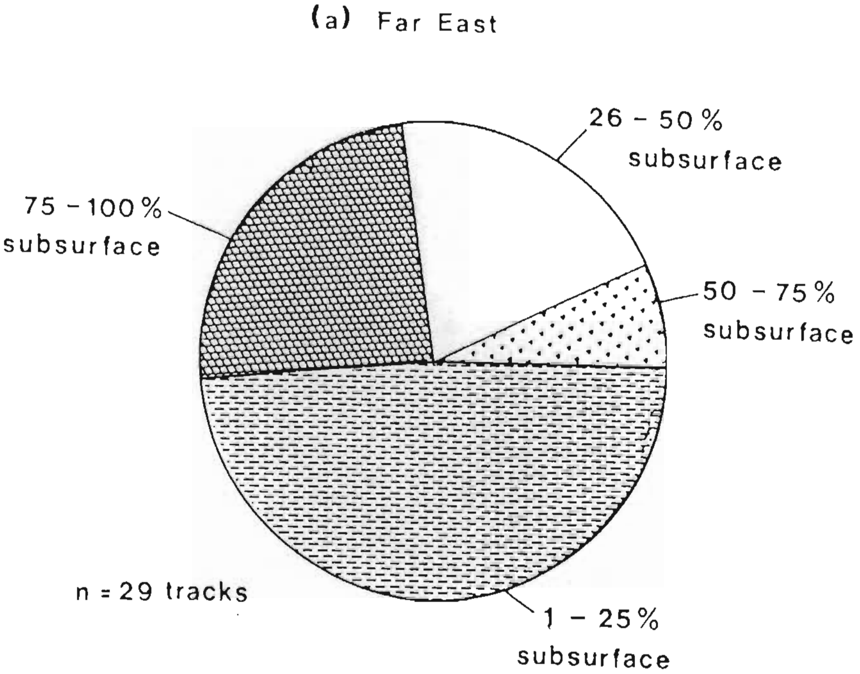


FIGURE 2.5: Length of foraging paths of *E.g.* *namibensis* measured at Far East (a) and Gobabeb (b).



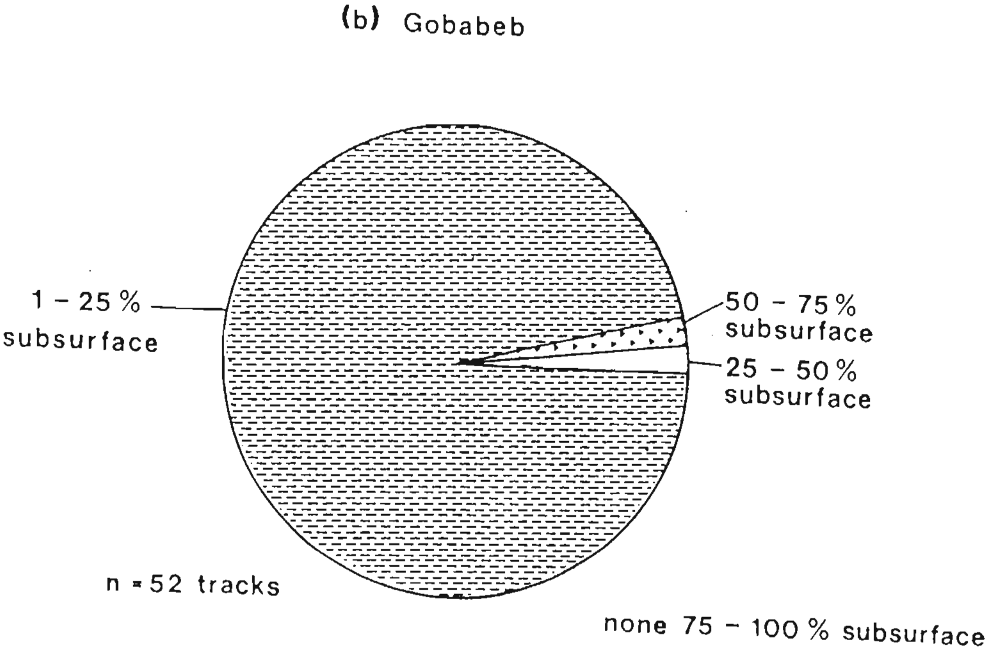


FIGURE 2.6: Proportions of surface to subsurface movement for foraging paths of E.g. namibensis measured at Far East (a) and Gobabeb (b).

2. Around the base of plants.
3. In areas of open sand where the individual is thought to have come across a termite concentration. Inspection of the sand in such localities often revealed presence of termite casts. This type of movement was termed 'area concentrated searching' (Plate 2.2).

At Far East, sandswimming was much more prevalent and not restricted to the three circumstances described above. Area concentrated searching was not recorded at the Far East site.

A frequency distribution of the angles of turn between successive moves of mole tracks is shown in Fig. 2.7. Since these turns had a circular distribution, it was not appropriate to analyse them by the usual statistical procedure of describing mean and standard deviation. Instead the mean angle $\bar{a}$ and the angular deviation (s), analogous to the mean and standard deviation respectively, were calculated for each distribution.

Tracks from both areas showed a strong directional bias with $\bar{a}$ being 0^{o} and 3^{o} for Gobabeb and Far East respectively. The mean angles for the two circular distributions were not significantly different (Watson-Williams test: $F=3.84$; $p>0.05$; d.f.=1,595) although the angular deviation was greater for the Far East group of tracks. The proportions of left to right turns were approximately equal and there were few large angles of turn illustrating clearly that foraging pathways seldom exhibited reversals of direction.

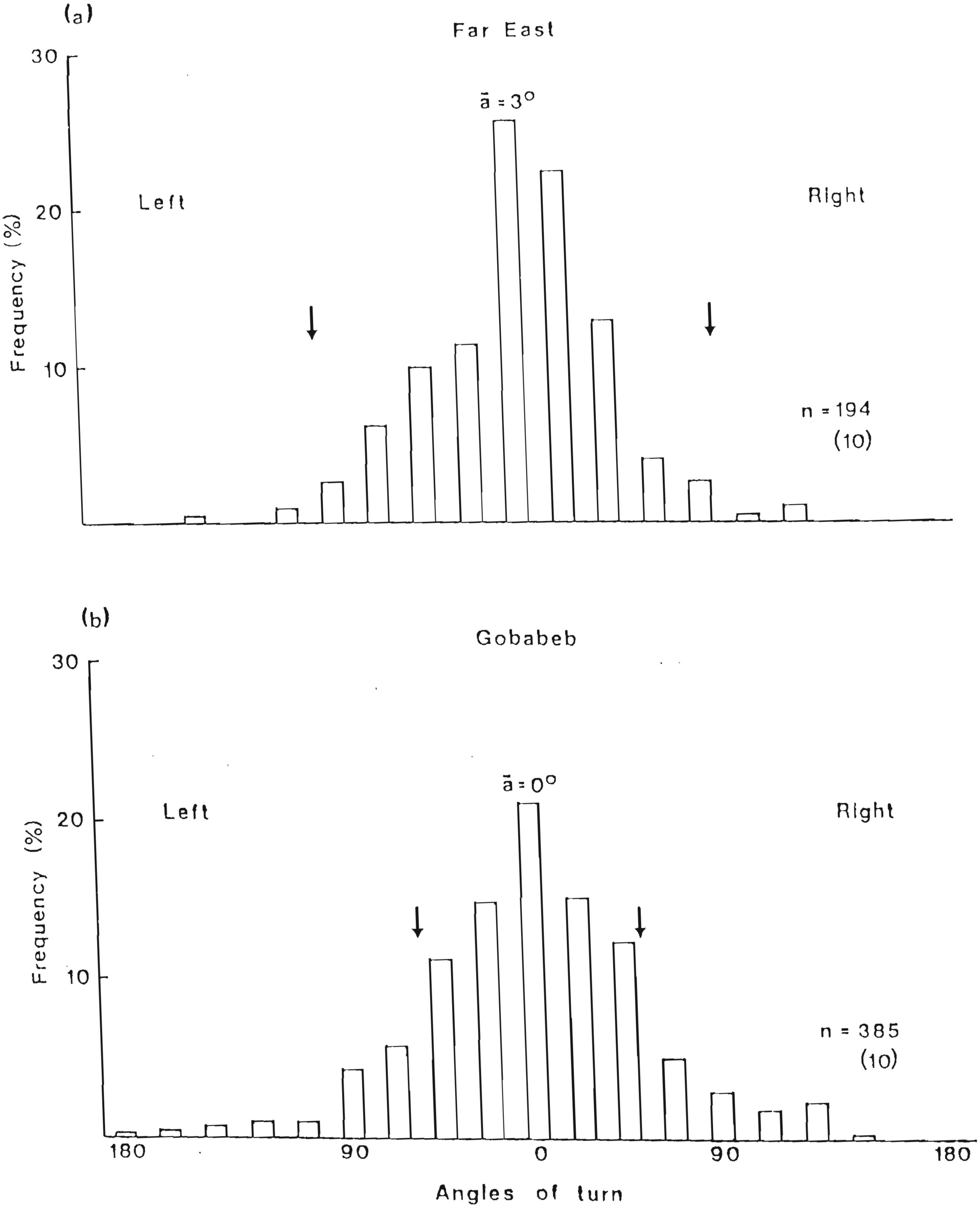


FIGURE 2.7: Turn angles between successive moves of foraging tracks of E.g. namibensis measured at Far East (a) and Gobabeb (b). Numbers in parentheses indicate number of tracks measured, arrows enclose angular deviations, $\bar{a}$ = mean angle.

The frequency distributions for move lengths between dips (Fig. 2.8) showed similar characteristics for both groups of tracks, peaking at short move lengths and with the longer move lengths occurring less frequently.

Because of the strongly skewed nature of the data, log 10 transformations were performed prior to any statistical testing (Table 2.3). Tracks at Gobabeb showed significantly more variation (variance ratio test: $F=1.80$; $p<0.001$; d.f.=377,203) than tracks at Far East due to the larger number of long moves but no significant differences were found between mean move lengths when employing Student's t-test corrected for unequal variances ($t_s=0.287$; $p>0.05$; d.f.=580).

The frequency histograms of move lengths (Fig. 2.8) and angles of turn (Fig. 2.7) failed to indicate whether moves or turns of given classes occurred in random sequences or whether there were any regularities in the sequences. For example, did left and right turns tend to alternate, or were short moves followed by short moves?

Move and turn sequences were analysed according to Smith (1974a). Members of pairs of move lengths in each track were classified as being either above or below the mean move length for the group of tracks to which it belonged in either the Gobabeb or Far East areas. The resulting frequencies were then entered into the following contingency table:

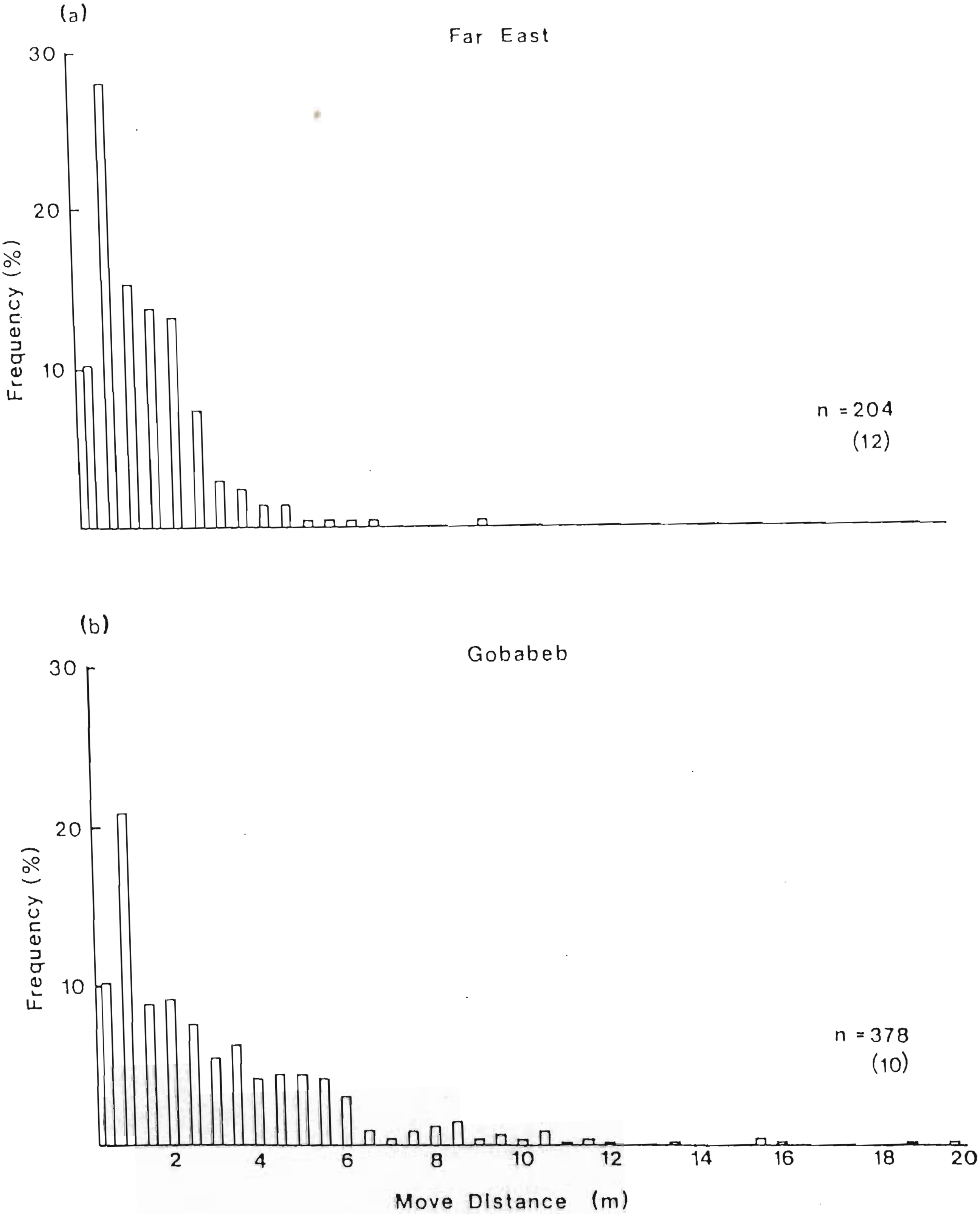


FIGURE 2.8: Move lengths of foraging tracks of E.g. namibensis measured at Far East (a) and Gobabeb (b). Numbers in parentheses indicates number of tracks measured.

TABLE 2.3: Mean distance (m) of move lengths for foraging paths of _E.g._ _namibensis_ measured at Gobabeb and Far East.

	Gobabeb	Far East
No. of tracks	10	12
No. of moves	378	204
Mean and variance		
$\overline{x}$	3.02	1.79
S	8.90	2.13
log $\overline{x}$	0.29	0.14
log S	0.18	0.10
antilog (log $\overline{x}$)	1.96	1.39
antilog (log S)	1.50	1.25

		Length of following move	
		above mean	below mean
Length of preceding move	above mean	a	b
	below mean	c	d

Chi-square tests were used to test whether move lengths that were above or below the mean tended to alternate when entries a and d fell below expectation, or cluster in like pairs when c and b fell below expectation.

The procedure for turn sequences was identical to that of the test described above except that turns were classified as being either left or right relative to the zero direction. The resulting frequencies were then entered into the following table which tested whether left or right turns tended to occur in pairs or to alternate.

		Direction of following turn	
		Left	Right
Direction of preceding turn	Left	a	b
	Right	c	d

Unfortunately, heterogeneity testing of chi-square for sequences in each individual track was not possible because of unavoidably small sample sizes in many instances. Thus results of chi-square testing (Table 2.4) are based on the assumption that all tracks from one particular area were homogenous in their turn and move sequences.

The evidence from the chi-square tests shows that for tracks in both localities, there was a significant tendency for moves

TABLE 2.4: Chi-square values (after Yates correction) resulting from performing sequence tests on the relations between successive moves and turns for foraging pathways of *E. g. namibensis*.

Area	No. of tracks analysed	Move sequences a	b	c	d		
Gobabeb	10	127	58	53	129	$\chi^2=55.93$	$p<0.001$
Far East	12	58	38	38	56	$\chi^2=6.81$	$p<0.01$
		Turn sequences					
Gobabeb	10	66	84	84	70	$\chi^2=4.98$	$p<0.05$
Far East	12	16	41	36	85	$\chi^2=3.36$	$p>0.05$

d.f. = 1 for all tests

above and below the mean to occur in like pairs, i.e. moles tended to follow short with short and long with long moves. Referring to Fig. 2.1, it is apparent that the shorter moves took place when moles were foraging near plants or in areas of the dunes where termites occurred, i.e. in association with 'area concentrated searching'. When travelling between plants or termite-rich localities, move lengths were increased.

Tracks at Gobabeb showed a clear alternation of left and right turns rather than like turns followed by like. The low chi-square value for the tracks at Far East indicate that turns happened in purely random sequences.

Fig. 2.9 illustrates the linear relationship between length of foraging pathways and number of plants encountered for the Gobabeb and Far East groups of tracks. The slopes of the two linear regression lines differed significantly (Student's t-test: $t=3$; $p<0.005$; d.f.=37) showing that the plant encounter rate at Far East was higher than that at Gobabeb.

The mean number of plants encountered per track at Gobabeb ($\bar{x}=19.11$; S.D.=16.02; $n=23$) and Far East ($\bar{x}=11.15$; S.D.=6.30; $n=13$) did not differ significantly (Student's t-test for samples with unequal variances $t_s=0.462$; $p>0.05$; d.f.=27,12).

The amount of subsurface movement around the base of plants encountered along the foraging tracks at Gobabeb is shown in Fig. 2.10. Relatively few plants had high foraging

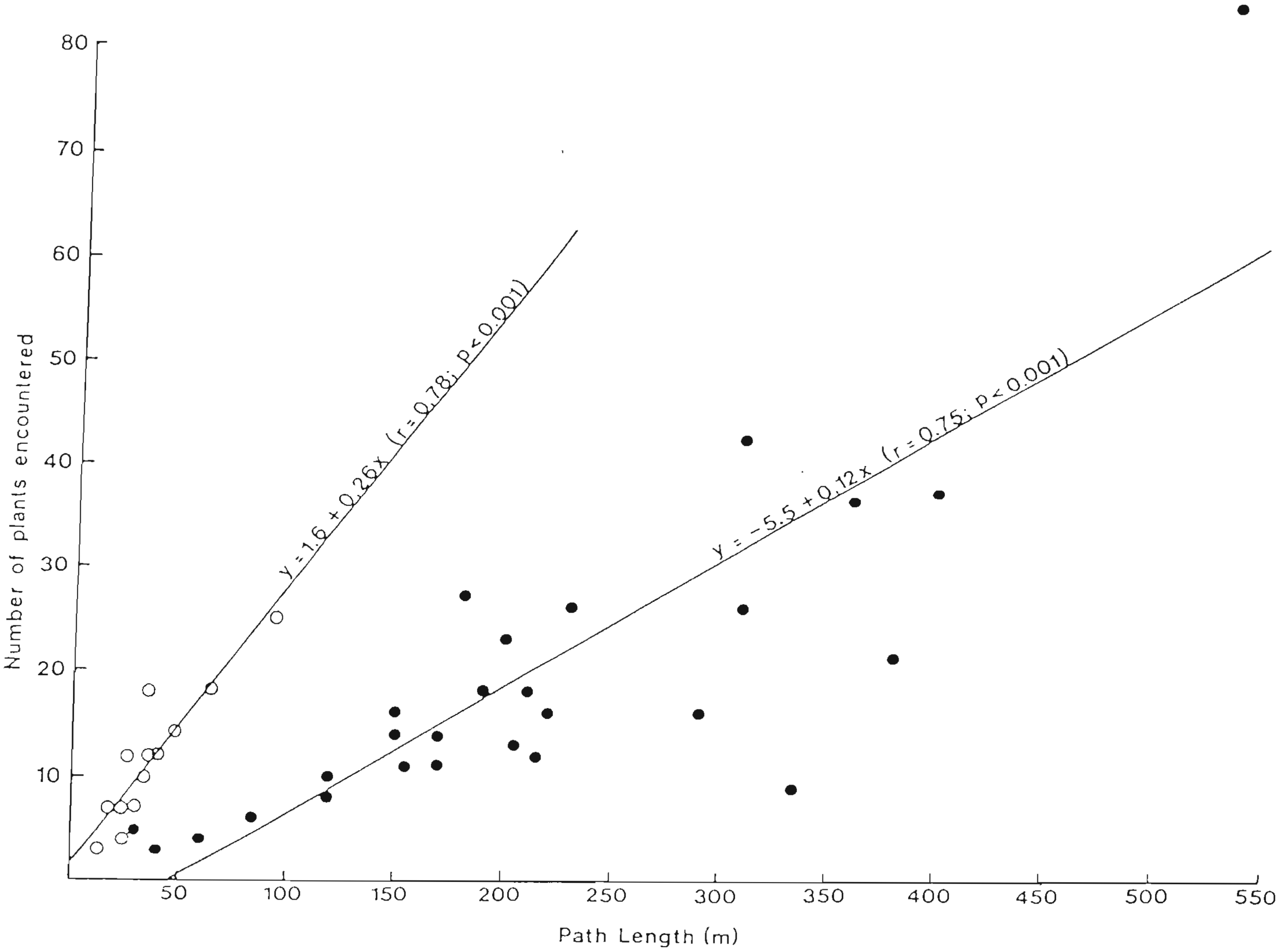


FIGURE 2.9: Relationship between length of foraging tracks and number of plants encountered at Far East (open circles) and Gobabeb (closed circles).

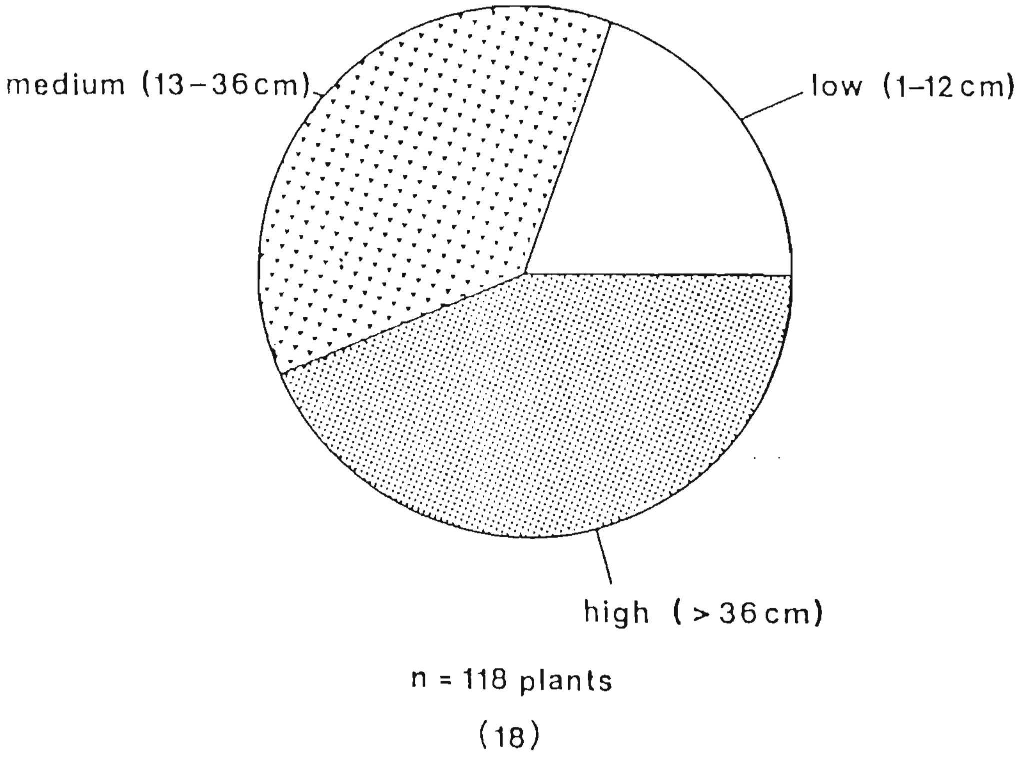


FIGURE 2.10: Foraging intensity (amount of subsurface movement) around base of plants encountered along foraging paths of *E.g. namibensis* at Gobabeb. Number in parentheses indicates number of tracks on which observations were made.

intensities, i.e. greater than 0.36m of sandswimming movement.

DISCUSSION

Dietary Composition and Feeding Preferences

From the results of stomach content analysis and laboratory observations on feeding behaviour, it is clear that *E. g. namibensis* is capable of taking a wide spectrum of prey, but under natural conditions feeds mainly on sedentary, soft bodied, psammophilous invertebrates such as termites and insect larvae. Holm (1969) whose work is the only other to document natural diet in *E.g. namibensis*, reported similar findings. Presence of plant material in stomachs of *E.g. namibensis* may have resulted from accidental ingestion whilst foraging amongst roots. However, Bateman (1961) and Kuyper (1985) recorded plant bulbs eaten by captive golden moles (*Amblysommus hottentotus*) suggesting that ingestion of plant material by chrysochlorids may not be entirely incidental.

The importance of termites in the diet of *E. g. namibensis* in comparison to the apparent paucity of termites in the Namib dunes indicates that moles are highly selective feeders, specialising on termites (and to a lesser extent insect larvae) in preference to more abundant prey items such as coleopterans and thysanurans. In light of the theoretical prediction that at low food abundances (such as those found in this study) food generalists should be favoured over food specialists (Nevo, 1979; Schoener, 1969), it appears paradoxical that *E. g. namibensis* should exploit such a scarce resource.

It is tempting to speculate that the predominance of termites and insect larvae in the diet of Namib moles is due to factors relating to the nutritional value and water content of these prey. Redford and Dorea (1984) found that termites and insect larvae, by virtue of their high fat content, are generally of higher nutritional quality than other types of invertebrates. Furthermore, insect larvae were found to have the highest water content of all the groups examined in this study. Other workers (Matsumoto, 1976; Redford & Dorea, 1984) have reported even higher water contents for termites, as great as 80% of the body mass in some species. Noy-Meir (1973) has pointed out that water content of food is often of primary importance in determining dietary habits in arid regions. This situation could apply to _E_. _g_. _namibensis_ which, having no access to free water, must rely solely on the moisture content of its food to remain in water balance.

Redford and Dorea (1984) argued that it is availability and abundance rather than differences in nutritional value that determine the type of prey taken by most invertebrate eating mammals. For example, the predominance of earthworms in the diet of the European mole (_Talpa_ _europaea_) is a reflection of soil fauna composition rather than actual food preferences (Funmilayo, 1977; Skoczen, 1966).

Unlike most arthropods, termites are social. This means that termites are usually grouped, creating a concentrated food source. This, together with the prevalence of termites in many habitats may explain why many animals feed opportunistically on them (Huey & Pianka, 1981; Perrin, 1980).

A question of crucial importance is, how ubiquitous are termites in the Namib dunes in relation to other potential prey items? Little information is available on the status or habits of the dune termite, P. a. silvestri recorded in the dunes at Gobabeb (Coaton & Sheasby, 1973; Holm & Scholtz, 1980). The paucity of knowledge on this species is probably a consequence of its elusive habits, resulting from a subterranean existence and extreme sensitivity to changes in humidity and temperature which has been reported for congeneric species by Krishna and Weesner (1970) and Lee and Wood (1971). However, the ample evidence of termite activity documented in this study, i.e. the frequent occurrence of termite workings, especially in association with plants, as well as the importance of termites as a food resource both for moles and other insect eating vertebrates such as lizards (Robinson & Cunningham, 1978) attests to the abundance of termites in the dunes. Since the role of termites as detritivores has been found to be of considerable importance in other arid ecosystems (Johnson & Whitford, 1975; Krishna & Weesner, 1970), it is likely that P. allocercus serves a similar function in the Namib dunes, feeding upon accumulations of windblown detritus and dead plant material that collect around clumps of vegetation.

For the reasons stated above, it is believed that termites are considerably more abundant than the results on prey availability data obtained from excavation samples indicate. This being the case, it is likely that the Namib mole is opportunistically feeding on a sedentary prey resource that occurs in patches of high concentrations, in preference to pursuing more active and mobile forms such as coleopterans and thysanurans. Similarly, as laboratory observations have shown, insect larvae, because of their sessile nature and soft body, are easier to catch and consume than adults of the same species.

Members of the Chrysochloridae in general, appear to be a family of opportunistic insectivores with interspecific discrepancies in diet, merely reflecting local variations in abundances of different components of the soil or sand fauna. For instance, earthworms form the major dietary component of species found in mesic environments including *Chrysochloris stuhlmanni* (Jarvis, 1974; Lamotte & Petter, 1981), *Chrysospalax villosus* (Smithers, 1983) and *A. hottentotus* (Kuyper, 1985; McConnell, 1986), whereas legless lizards and insect larvae are predominant in the diets of *Chryptochloris wintoni* (Roberts, 1951) and *E. g. granti* (Shortridge, 1942), both found in the sand dune habitat of the south western Cape Province near Port Nolloth. Such dietary flexibility is characteristic of other groups of subterranean insectivores such as the European and North American talpid moles (Godfrey & Crowcroft, 1960; Raw, 1966; Rust, 1966; Whitaker, Maser &

Pederson, 1979) and is probably as a response to the generally low food abundances (both plant and animal), typical of the subterranean ecotype (Nevo, 1979).

Resource Abundance and Distribution at Gobabeb

Much attention has been focused on the abundance and diversity of the Namib dune fauna, especially the large endemic populations of diurnal tenebrionid beetles (Koch, 1961; Lawrence, 1959; Robinson & Seely, 1980; Seely, 1978). However, no studies have specifically addressed the quantification of sand dwelling arthropod fauna, although Seely and Louw (1980), have calculated a figure of $0{,}01\text{gm}^{-2}$ for overall animal biomass in the Namib dunes. This figure is the lowest reported for any terrestrial ecosystem and is representative of a typical low rainfall year as was the case during the period of this study. The low values for invertebrate biomass obtained in this study concur with the findings of these authors, and furthermore demonstrate the patchy distribution and extreme variability of this resource base.

Wiens (1976) defines patches as 'non-random distributions of resource utilization among environmental units'. Plants, because they provide both a sheltered microenvironment and food (Holm & Scholtz, 1980; Larmuth, 1979; Seely, De Vos & Louw, 1977) are centres of termite activity and harbour both a greater number and variety of organisms than do areas of open sand. Indeed, the biomass of invertebrates excavated from beneath vegetation clumps was one hundredfold that of unvegetated areas. Such vegetation clumps together with areas of termite concentrations found in open sand can therefore be considered as patches of high prey availability. The fact that *S. sabulicola*, *T. hereroensis* and *C. spinosa* together cover less than 5% of the dune slope (Boyer, 1987) further serves to emphasise the patchiness of resource distribution.

Movement Patterns of Moles at Gobabeb

Differences in prey dispersion influence both foraging tactics and foraging pathways (Smith 1974a, 1974b). Considering that *E. g. namibensis* favours prey that are sessile and patchily distributed, one would expect them to exploit patches of high resource availability such as vegetation clumps, and furthermore to have developed a foraging behaviour that will be effective in encountering such patches and which will minimise the energetic costs of travelling between patches.

The movement patterns described for moles have at least one important consequence. Both the restriction on the occurrence of large turns and the tendency for left and right turns to alternate are effective in taking the mole into unsearched ground. On only one occasion of the ten paths mapped at Gobabeb, did moles cross their foraging tracks. It is of advantage for an animal not to search the same area twice in an environment where food is sparsely distributed.

In such a situation, return time regulation is of significance. Cody (1971) defined return time as 'time which elapses between successive visits to points'. Gill and Wolf (1977) have shown that in hummingbirds, timing of visits to flowers is a compromise between maximising nectar accumulation and minimising loss to other individuals. Similarly one would expect moles to utilise their home range in such a way that the average return time to patches has evolved as a balance between allowing resources (emerging or reproducing insects) to renew and preventing loss to other moles. Unfortunately, return times were not determined in this study due to difficulties experienced in following individual moles over long periods of time. The small amount of data obtained at Gobabeb indicated that return time took several days, since tracks monitored for three days did not return to the same patches (Chap. 3).

The strong onward going nature of the foraging paths together with the observation that plants were often bypassed within a metre or less of a dip, indicates that encounters with patches are purely stochastic events, and that the moles' ability to detect patches of prey is effective over short distances only. Tactile, olfactory and auditory cues as well as sensitivity to vibrations are known to be important in prey detection in other subterranean insectivores (Eloff, 1951; Kuyper, 1985; Mellanby, 1971; Quilliam, 1966). The function of the foraging dip, although obviously important to prey detection, is not clearly understood. Laboratory observations indicated that vibrations resulting from prey moving in the sand could be detected by E. g. namibensis when it dipped into the sand. Furthermore, Nolte (1968), reported that the ear ossicles in E.g. namibensis are disproportionately large, particularly the malleus, suggesting that the mole is very sensitive to vibrations. However, the possibility that other types of substrate information may be important in prey or patch location, such as moisture content of sand, presence of organic matter, termite casts or shallow roots which sometimes radiate out 2m from the base of plants (field observations), cannot be ignored.

Once a patch was encountered, the move lengths between dips were shortened, thus effectively keeping moles in patches after they had been located. Often in such situations, moles switched from surface movement to area concentrated sandswimming behaviour in response to high prey availabilities such as in areas of termite concentrations. Move lengths were longer between patches, so that the moles travelled rapidly between clumps. Such movement between clumps is obviously far less energetically expensive than sandswimming, although at the expense of less efficient foraging since prey location does not appear effective when moles are emerged on the sand surface.

The number of patches encountered by an individual was dependent on the length of the foraging path. Laboratory studies (Chap. 4) have shown that when food supply was restricted, moles exhibited extremely high surface activity scores. Thus under field conditions it is likely that moles continue to forage until their energy requirements have been satisfied, and path length depends on how many 'profitable' patches are encountered. The extremely variable biomass values obtained from plant excavation sampling highlights the unpredictability of resources within patches. Theory predicts that if one patch type is much worse than others, the animal should stop foraging in that patch (Pyke, 1984). The variation in foraging intensities at different patches by moles seems consistent with this assumption.

Search Paths of Moles at Far East

E. g. namibensis is common prey of the owls Bubo africanus and Tyto alba (Nel, 1969; Skinner, Lindeque, Van Aarde & Dieckmann, 1980; Tilson & Le Roux, 1983), and it is possible that the movement patterns described could easily be interpreted as a response to avian predator avoidance as is the case with foraging behaviour in desert rodents (Kotler, 1984; Thompson, 1982). The problem of whether a particular movement pattern is specifically adapted to locating food can only be answered if movement patterns are considered in relation to the food supply of the forager. Differences between movement patterns of moles at Gobabeb and Far East appear to be an effect of differences in prey distribution rather than changes in predator risk.

Although no significant differences were found between the two areas in insect biomass and occurrence of termite casts in vegetation clumps, resource distribution at Far East can be considered as more abundant and predictable by virtue of the higher vegetation densities. Move lengths and distance of foraging paths were shorter as a result of higher patch encounter rates as opposed to a decrease in the number of patches visited. Consequently, because moles need not travel as far, they can afford to spend more time engaged in the energetically expensive but more effective prey locating sandswimming movement. No difference was found in the directionality of movement patterns although the turn sequence did differ. The reason for this is not known, but is probably a reflection of subtle variations in vegetation distribution. As Pyke (1984) has pointed out 'there are as yet no predictions as to exactly what the directionality, or more generally, the rules governing patterns of movement should be in different situations'.

CONCLUSIONS

It appears that the foraging behaviour of the Namib mole has evolved directly in response to an environment where resources are sparse and patchily distributed. Namib moles specialise on a prey that is non-vagile and clumped in distribution, thus avoiding the high energy costs implicit in pursuing single fast moving prey items. Although totally blind, Eremitalpa has developed a search pattern effective in encountering patches of high prey availability. Furthermore, when moles do encounter areas of high food returns, only then is surface movement switched to the far more energetically expensive sandswimming behaviour.

The sandswimming of *E. g. namibensis* is analogous to the temporary shallow subsurface runs common to chrysochlorid burrow systems (Roberts, 1951; Smithers, 1983). Occasional surface activity recorded for other chrysochlorids occurs in situations where soil compaction due to dry weather conditions, makes burrowing difficult (Kuyper, 1979), or conversely after heavy rainfalls (Lamotte & Petter, 1981). However, the giant golden mole (*Chrysospalax trevelyani*) is the only chrysochlorid apart from *E. g. namibensis* to forage almost exclusively on the surface (Maddock & Hickman, 1985). Here again, surface activity is interpreted as an adaptation to reduce the energetic costs of foraging. Since the energy requirements for burrowing increase with body size (Vleck, 1981), the cost of foraging below ground for an animal the size of *C. trevelyani* must be prohibitive.

CHAPTER 3

MOVEMENTS AND HOME RANGE

INTRODUCTION

Namib moles are largely nocturnal and have seclusive burrowing habits which make them difficult to observe directly in their natural habitat. Not surprisingly, no direct information has been gathered on the general behaviour of moles in the wild, although a few general observations have been made on laboratory maintained animals (Holm, 1969; Meester, 1964).

Radioactive tagging has been used with some success to study subterranean insectivores in the field (Godfrey, 1955, 1957; Kuyper, 1979), as has radio telemetry (Maddock & Hickman, 1985; Stone & Gorman, 1985). However, small radio transmitters implanted in E. g. namibensis caused a deviation in normal behaviour patterns (Appendix A). Furthermore, small detection range of radio isotopes, although useful for monitoring movements of animals in discrete underground burrow systems, restricts the use of this technique on a wide ranging surface forager such as E.g. namibensis (Wolton, 1985). On the other hand, less sophisticated techniques involving behavioural artefacts such as, observing construction of mole hills (Hickman & Brown, 1973) or the repair of flattened tunnelways (Hamilton, 1939; Arlton, 1936) has allowed the determination of periods of digging activity in fossorial mammals. The present study demonstrates the feasiblity of using surface tracks made by Namib moles to augment conventional capture, mark and recapture methods as a technique for providing insight into:

1. Population density of moles.
2. Home range size, stability and overlap.
3. Home range utilisation and nesting behaviour.
4. Territoriality.

MATERIALS AND METHODS

Study Area

The study site was situated 8km S.E. of Gobabeb on an eastward facing dune slope. This area was relatively homogeneous in biotic and physical characteristics and typical of the dune plinth zone described by Robinson and Seely (1980). Vegetation was sparse with dominant plants being the dune endemic grasses *Stipagrostis sabulicola* and *Eragrostis spinosa*, and the dune succulent *Trianthema hereoensis*. These three species frequently formed large hummocks 1-2m high, where large accumulations of windblown detritus were found.

Location, Tracking and Capture of Moles

The Namib mole is a surface forager, hunting prey on the dune surface at night while spending daylight hours buried to depths of 5-35cm (Chap. 5) in soft dune sand. Mole tracks thus provide a clear and easily followed record of an individual's movements on the dune surface during nocturnal foraging periods.

A grid system of numbered posts was used to facilitate monitoring of mole movements and population size. The grid (total area 58.5ha) employed had a cell size of 50 x 50m (0.25ha) and measured 26 cells (y axis: 1300m) by nine cells (x axis: 450m) with the long axis of this grid running parallel to the length of the dune. The dune crest and interdune valley were not included in the grid area.

Mole tracks present on the study grid were monitored two to five days per month from July 1983 to July 1984. The number of mole tracks recorded on any one particular day on the grid was taken as representing the number of moles active during the preceding 24 hours, since the dune surface was cleared daily by the natural effects of wind and sand movement. All tracks encountered were followed to their termination and their position plotted onto a scale map of the study grid. Sampling days were not necessarily consecutive due to inclement weather conditions, particularly wind, and occasionally rain, both of which obliterated tracks. Searching for tracks early in the morning (sunrise to 10h00) was found to be the most successful strategy, since later in the day dune surface glare and windy conditions made location of tracks difficult. Nighttime searching for tracks was avoided to minimise disturbance during the main period of nocturnal activity.

Moles were captured using the follow-and-dig method (Chap. 1). Body mass and sex of captured individuals were recorded and animals marked by toe clipping prior to releasing at the point of capture. The success of this follow-and-dig method varied, with animals located underneath plant hummocks generally more difficult to retrieve than moles submerged in unvegetated sand. Consequently, only a few of the tracks followed on each sampling day resulted in successful location of animals, with an average of one mole caught for every five tracks followed. Occasionally moles were caught using drift fence and pitfall traps (Chap. 1). Although an 80% success rate was achieved using this method, the procedure was labour intensive and considered impractical to use on a regular basis.

Captures and any subsequent recaptures of marked individuals were each given a coordinate corresponding to one cell of the grid, for example 15x/6y. In addition, grid coordinates were assigned to tracks if known to belong to a marked mole (confirmed by capture). Estimation of home range used one of the simplest methods available, the minimum area method (Macdonald, Ball & Hough, 1980; Southwood, 1978), despite some of its inherent problems (see discussion). The centre point of all used cells for an individual were marked and a line drawn around these locations, such that it enclosed the smallest convex polygon. The resultant area was measured with a planimeter.

RESULTS

Captures and Numbers in the Population under Observation

Population size in small mammals can be estimated by many methods, but often the Peterson method or its derivatives are employed (Caughley, 1977; Southwood, 1978), or alternatively a direct enumeration model using the minimum number of animals known to be alive (M.N.A.) (Krebs, 1966). Such methods require that consistent sampling efforts be made at regular intervals during the study and that the catchability of all members of the population is equal. These requirements could not be met by the present study since regular trapping was impracticable and the efficiency of capture by hand was variable. Population estimates were thus made by two alternative methods:

1. Mole abundance between July 1983 and July 1984 as estimated by the number of individual tracks counted on the study grid is shown in Fig. 3.1. The results indicate a fairly stable population size with an average of 9.68 (n=38; S.D.±2.99) tracks counted per night.
2. Estimate of population size using the track method was supplemented by an estimate of the residential population obtained by counting the number of individuals caught more than once in the study area (Reeve, 1982). Data on 16 captured moles is given in Table 3.1. All were adults with the possible exception of one female (No. 14) which was probably a subadult based on body mass measurement. The number of recaptured animals indicates a population size of about 11 individuals within the study area over the period November 1983 to July 1984, a figure close to the 9.7 derived from counts of tracks. A population density of between 0.17 to 0.19 moles ha^{-1}

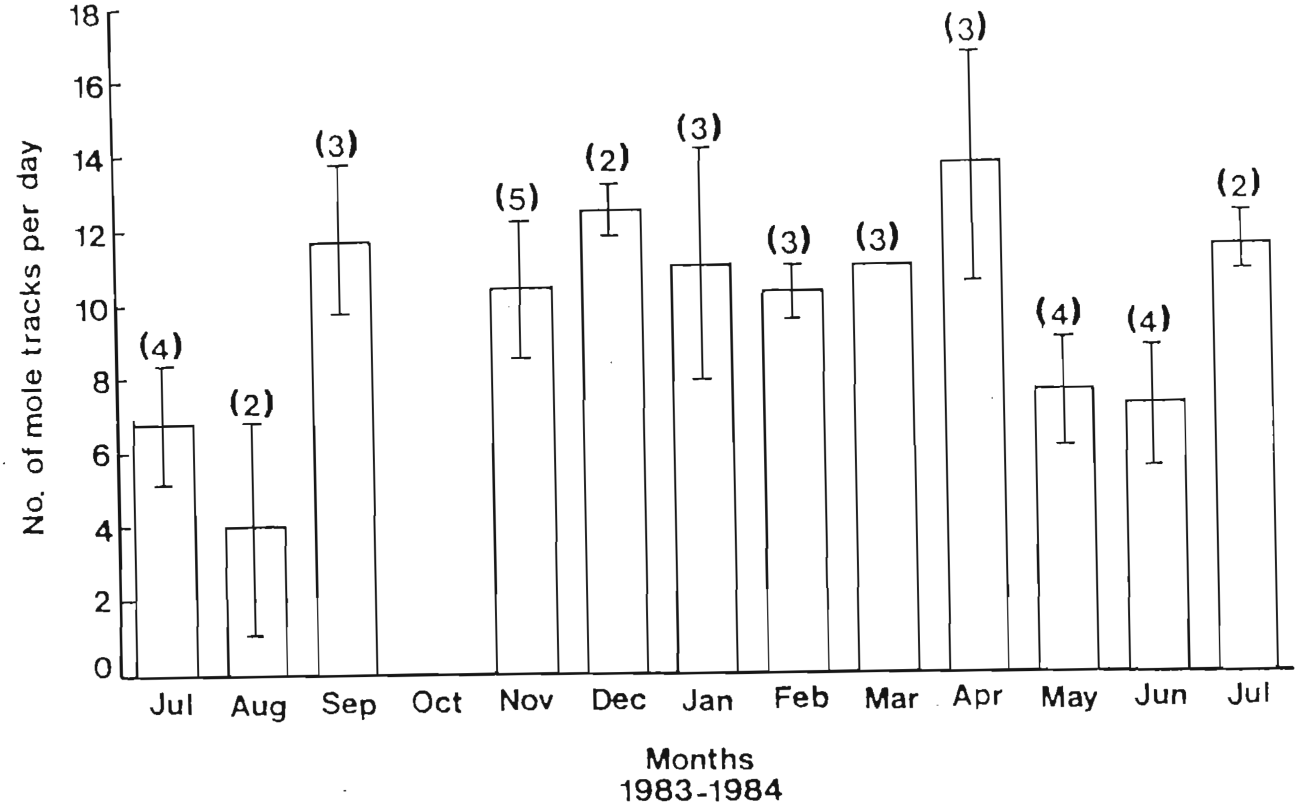


FIGURE 3.1: Number of mole tracks on the study grid at Gobabeb. Columns represent mean values, lines indicate standard deviations, numbers in parentheses give number of days that tracks were counted. No data were collected for October 1983.

TABLE 3.1: Captures, locations and home ranges of individual <u>E.g.</u> <u>namibensis</u> at Gobabeb.

No.	Sex	Mass (g)	No. captures	Date of capture First	Date of capture Last	Time[a] (days)	No. of[b] locations	H.R.[c] (ha)
1	M	27	4	13.11.83	7.5.84	176	20	7.16
2	F	22	6	14.11.83	18.11.85	734	24	2.20
3	M	26	3	14.11.83	17.11.85	733	3	-
4	M	30	1	21.11.83	-	-	1	-
5	M	26	3	13. 1.84	16. 2.84	35	15	3.10
6	F	21	3	13. 1.84	17. 2.84	36	3	-
7	F	22	3	16. 1.84	15. 2.84	31	17	1.80
8	M	29	2	16. 1.84	24. 1.84	10	11	-
9	M	27	1	6. 2.84	-	-	1	-
10	F	22	4	6. 2.84	19. 7.84	164	15	3.94
11	F	18	3	2. 3.84	13. 5.84	72	12	1.95
12	M	25	4	6. 5.84	19. 7.84	74	26	12.30
13	F	23	3	6. 5.84	20. 9.84	137	11	4.59
14	F	15	1	13. 5.84	-	-	1	-
15	F	20	1	29. 6.84	-	-	1	-
16	F	20	1	19. 7.84	-	-	1	-

[a] Time elapsed between first and last capture

[b] Grid locations obtained from capture points and track positions

[c] Home range

thus appears a reasonable estimate.

Home Range Size, Stability and Overlap

Home range area was measured for eight adults, all of which had been caught three or more times and for which a minimum of 11 grid locations had been obtained (Table 3.1, Fig. 3.2). The size of the areas frequented by moles varied greatly. In order to ascertain whether this variability was significantly dependent upon the number of surveys carried out on every animal, the Spearman's rank correlation coefficient was calculated between the size of home ranges and the number of captures of each mole ($r=0.45$; $p>0.05$; d.f.=6), the number of grid locations for each mole ($r=0.45$; $p>0.05$; d.f.=6) and the number of days elapsed between first and last capture for each mole ($r=0.48$; $p>0.05$; d.f.=6). Since the results of these statistical tests did not reveal any significant correlations, the importance of the three variables under examination was eliminated from the final demarcation of home range area.

Small sample size precluded reliable statistical verification of differences between male and female range size, thus mean home range area for eight adult moles was calculated as 4.63ha (S.D.$\pm$3.57). However, inspection of the data suggests that ranges of males (3.10 - 12.30ha) were larger than those of females (1.80 - 4.59ha).

Home ranges did show a considerable degree of spatial overlay (Fig. 3.2), although the amount of temporal overlap was difficult to determine on the basis of the collected data.

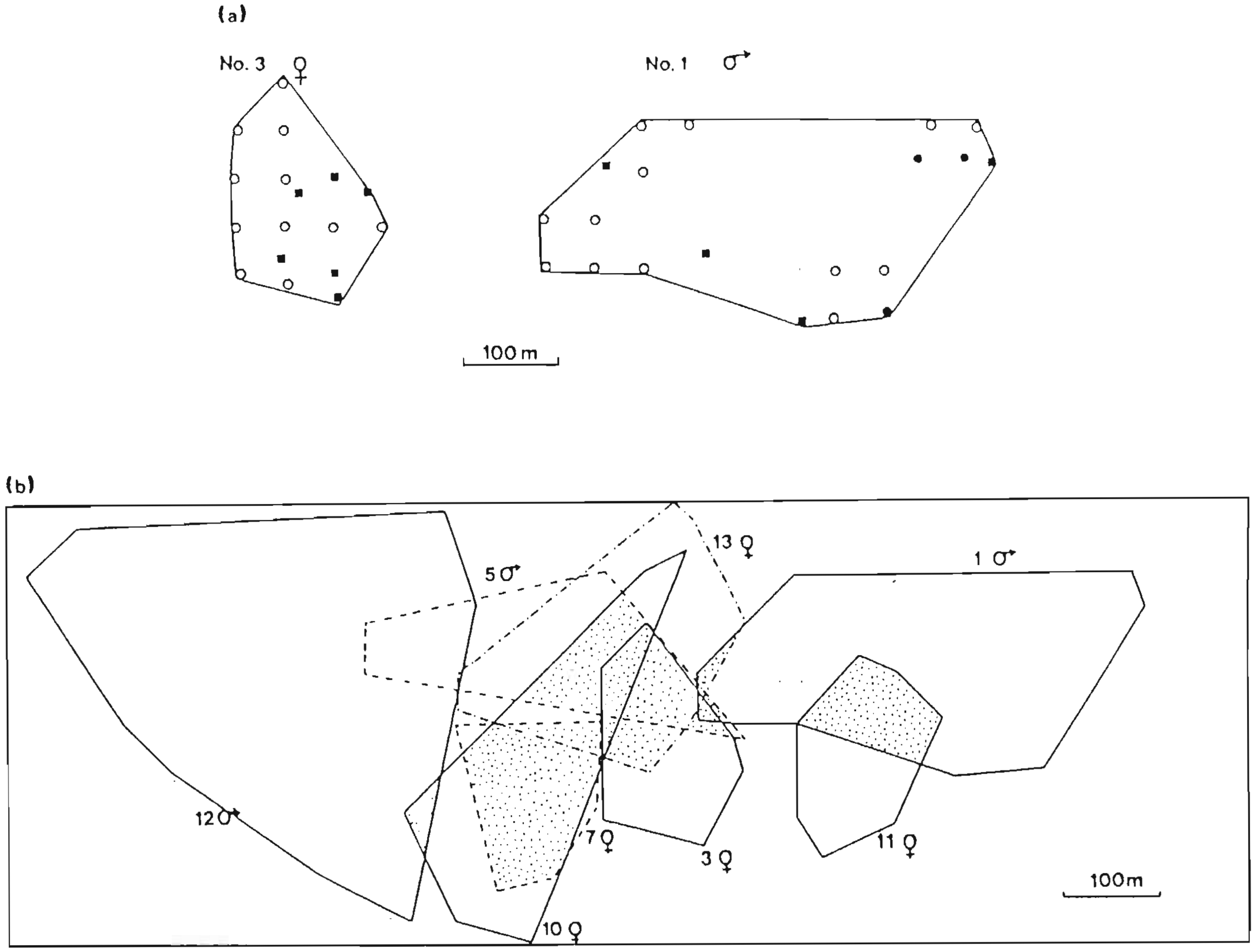


FIGURE 3.2: (a) Example of home range estimation for two adult E.g. namibensis at Gobabeb. Squares represent capture sites, closed circles rest sites and open circles track locations. Boundaries delineated by minimum area method. (b) Home ranges of eight adult E.g. namibensis measured between November 1983 and November 1985 at Gobabeb. Stippled portions indicate areas of temporal overlap between ranges, the rectangle delineates the perimeter of the study grid.

Shaded portions indicate areas of overlap between animals which were known to be present on the study site within the same time period. For example, female No. 13 was recorded on the study site between May and October 1984 and thus overlapped in time with male No. 3 (November 1983 - November 1984) and female No. 10 (February - July 1984), but not male No. 5 (January - February 1984) (Fig. 3.2, Table 3.1).

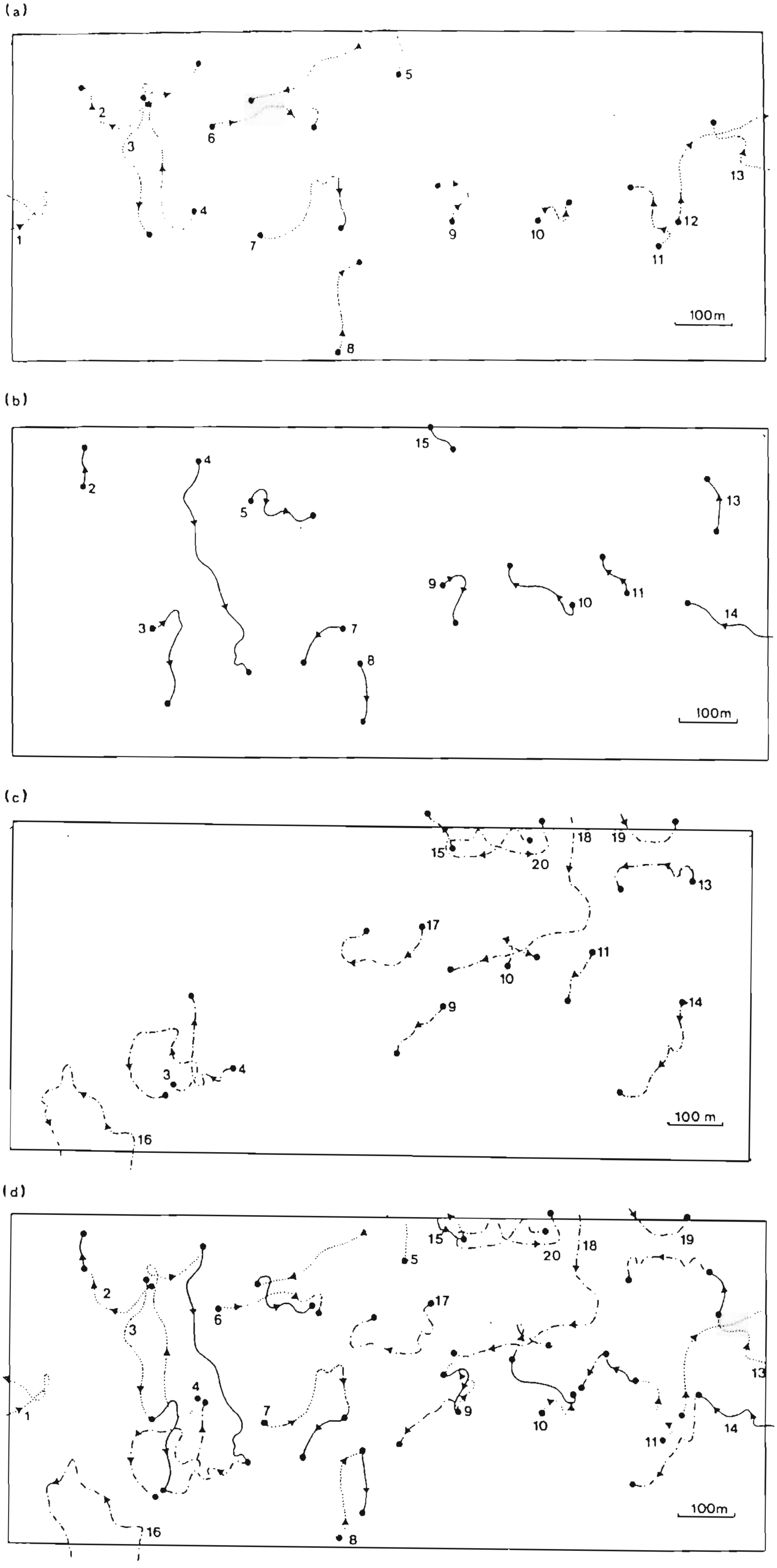
Moles appeared to show a marked tendency to remain in the same general locality from year to year, as for example moles Nos 2 and 3 (Table 3.1) that were relocated on a subsequent field trip to the study site in November 1985, within 100m of their initial capture point two years previously.

Movement Patterns and Position of Rest Sites

Nearly all movement occurred at night and was of a nomadic nature with individuals changing 'rest' sites every day. A 'rest' site refers to the place where moles buried themselves in the sand after cessation of nocturnal surface activity, and where they usually remained till the following evening.

A typical example of nightly movement patterns of moles is shown in Fig. 3.3, which illustrates the position of surface tracks recorded on the study grid over three consecutive days, 5-7 September 1983. Tracks of 13 individuals were located on day one (Fig. 3.3a) (Nos 1-13). Day two (Fig. 3.3b), 11 tracks were recorded including new paths for Nos 2, 3, 4, 5, 7, 8, 9, 10, 11 and 13, and those of two animals Nos 15 and 14 that had moved onto the study grid from peripheral areas.

FIGURE 3.3: Movement patterns of E.g. namibensis at Gobabeb on 5th (a), 6th (b), and 7th (c) of September 1983, with the cumulative record of three nights of activity shown in (d). Numbers refer to tracks made by different individuals, circles indicate rest sites and arrows direction of movement. The rectangle demarcates the perimeter of the study grid.


(a)
5
2
6
3
4
1
7
9
10
12
11
13
8
100m
(b)
15
2
4
5
13
9
10
11
14
3
7
8
100m
(c)
15
20
18
19
13
17
11
10
9
14
4
3
16
100 m
(d)
15
5
20
18
19
2
6
17
3
13
4
7
9
1
10
11
14
16
8
100m

Movements of Nos 1 and 12 were not monitored since they had moved off the grid on day one, while no fresh tracks were located for No. 6. On day three (Fig. 3.3c), four new moles moved onto the study grid (Nos 16, 18, 19 and 20), while Nos 2 and 8 moved off. No new tracks were detected for Nos 5 and 7, but 3, 4, 9, 10, 11, 13, 14 and 15 had all been active on the dune surface. A fresh set of tracks (No. 17) was found in the centre of the grid area, indicating that this individual had not been active on the surface for the two preceding days.

On any one particular night, foraging paths seldom traversed those of a neighbour. When track crossings did occur, there was rarely evidence of any direct encounter between the two animals concerned, suggesting that such crossings were usually temporally separated during the night. A cumulative record of three days of mole activity on the study grid showed clearly discrete centres of foraging activity between individuals (Fig. 3.3d).

Numerous excavations of rest sites (at least 100) during the course of this study, never revealed any evidence of nest material or any form of permanent burrow, chamber or tunnel construction. However, situation of rest sites was clearly linked to that of vegetation coverage. For 88 recorded rest site positions, 81.9% were located beneath plant hummocks and only 18.1% in areas of unvegetated sand. Rest site sharing between two or more individuals was never observed, and instances of return to a previous rest site by the same individual were rare. Only three cases of a rest site being used again were recorded during the one year study period, which included 38 sampling days and 359 observations of tracks.

DISCUSSION

Home Range Estimation

Home range indicates the area used by an animal during its normal activities exclusive of unusual erratic wanderings (excursions), migrations or emigrations (Brown & Orians, 1970; Burt, 1943; Jewell, 1966). During the present study, it was not possible to distinguish between normal activities and excursions of moles, hence no attempt was made to separate the two.

Home range can be calculated in a variety of ways. No attempt is made here to review all the methods available, since the pertinent literature is extensive, and no procedure is free of problems (for reviews see Anderson, 1982; Jenrich & Turner, 1969; Macdonald et al., 1980; Sanderson, 1966; Voigt & Tinline, 1980). The minimum area method (using a convex polygon) was deemed the most suitable and sufficiently precise for the data in this present study. The technique has historical prominence thus facilitating comparisons with many other small mammal species; it is non-parametric and hence not reliant on the assumptions of bivariate normality inherent in the probability ellipse technique (Jenrich & Turner, 1969); finally it is quick and simple to calculate and graphically easily represented. Alternative non-parametric methods are somewhat more mathematically complicated (Anderson, 1982; Ford & Krumme, 1979), but do not necessarily give greater biological insight.

Disadvantages of the minimum area method include, firstly, sample size bias. Usually the estimated size of the home range is heavily dependent on the number of observations obtained (Anderson, 1982; Haugen, 1942; Macdonald *et al*. 1980; Reeve, 1982). Because of the great variation in home range size between moles, it was difficult to assess how many grid locations were required to fully reveal an animal's range. Nevertheless, since no correlation was evident between the size of home ranges and the number of observed grid positions for different individuals, it was concluded that sample sizes used in this study (11-26 locations per individual) did not seriously affect the estimation of home range area.

Secondly, the shape of the home range is depicted as a convex polygon and may thus include large areas never frequented, especially if an animal's range is an irregular shape perhaps delineated by topographical features of a heterogeneous habitat (Wolton, 1985). For instance, Attuquayefio, Gorman and Wolton (1986) have demonstrated that home range shapes of the woodmouse, (*Apodemus sylvaticus*), are much more uniform in sand dunes in comparison to the much more complex shapes found in woodland. Since the study site at Gobabeb was specifically chosen for its uniformity in vegetative and topographical features, the shape of home ranges of _E.g. namibensis_ was unlikely to have been much affected by environmental heterogenity.

Home Range Size and Population Density

Intuitively, the home range will be the minimum area necessary to provide the key resources required by an individual. What constitutes a key resource may differ between different segments of the population, but amongst adult vertebrates, it is generally accepted that a primary determinant of home range size is likely to be access to food (Mace, Harvey & Clutton Brock, 1983).

If this is so, habitat productivity and the animal's energetic requirements (the latter being largely determined by body size) should be major factors effecting home range area. It is not surprising to find, therefore, that among different species of mammals, there is a clear relationship (McNab, 1963) between average home range size (A) and body mass (W) in the form of:

$$A = a.W^b$$

The value of the exponent b varies, depending not only on the diet of the animals involved, but on the type of statistical regression used. Currently there is much controversy as to which is the best statistical treatment and as to the biological significance of the resultant exponents (Harestad & Bunnell, 1979; Jenkins, 1981; Lindstedt, Millar & Buskirk, 1986; Mace *et al*., 1983; McNab, 1963). However, as Lindstedt *et al*. (1986) cautioned, allometric equations are not precise predictive laws, but merely describe patterns. Thus for the purposes of this discussion, it is sufficient to note that on the basis of body mass, *E.g. namibensis* would be expected to have a home range smaller in size than those of other subterranean insectivores. To the contrary, the mean estimate of home range size obtained for *E.g. namibensis* is without exception, several times larger than those reported for other subterranean insectivores (Table 3.2).

Studies carried out in association with the present investigation (Chap. 2) together with the work of Seely and Louw (1982) have demonstrated that both primary and secondary production in the Namib dunes are among the lowest reported for any terrestrial ecosystem. Large home range size in Namib moles is thus believed to be a necessity to ensure acquisition of sufficient invertebrate prey to satisfy energy demands, in spite of these animals having a very low metabolic expenditure in the field (Chap. 6). Similarly, home ranges of other mammals inhabiting desert regions are typically larger than those of mesic dwelling counterparts (Attuquayefio *et al*., 1986; Boulière, 1954; Petter, Lachiver & Chekir, 1984), an effect largely believed to be due to the low productivity of desert environments (McNab, 1963).

Species that inhabit low resource environments usually cannot maintain locally dense populations because of the limited

TABLE 3.2: Mean home range size of some subterranean insectivores. Sample size given in parentheses.

Species	Body mass (g)	Home range (ha)		Reference
		Male	Female	
Chrysochloridae				
Eremitalpa granti namibensis	21	7.52(3)	2.90(5)	This study
Amblysommus hottentotus	66	0.02(2)	-	Kuyper 1979
Talpidae				
Talpa europaea	65-120[a]	0.02(1)	0.01(1)	Godfrey 1955
		0.03(3)	0.04(10)	Haeck 1969
		0.60(1)	0.21(3)	Stone & Gorman 1986
Scalopus aquaticus	50-170[a]	1.09(4)	0.28(3)	Harvey 1976
Scapanus orarius	50-170[a]	0.15(1)	-	Schaefer 1981

[a] Body mass range obtained from Walker (1968).

amount of energy within a given area. Unfortunately a precise estimate of the population density of E. g. namibensis at the study site was not possible, but it does seem very much lower than the range of 2-50ha^{-1}) reported for Talpa europaea (Godfrey & Crowcroft, 1960; Haeck, 1969), reflecting the low carrying capacity of the Namib dunes.

Nesting Behaviour

During the course of the study, moles characteristically foraged in different parts of their ranges each night and were seldom observed to return to the same rest site occupied the previous day, although sometimes animals did remain buried and inactive at the same rest site for at least two days. The propensity for rest sites to be located beneath vegetation hummocks may serve for protection against terrestrial predators, since Holm (1969) observed that the genet (Genetta genetta), and the black-backed jackal (Canis mesomelas) follow trails and occasionally dig for moles. Resting under vegetative cover may also be involved with the avoidance of high daytime sand surface temperatures (Chap. 5).

Failure in this and other studies (Haacke, 1963; Holm, 1968) to find any form of permanent tunnel or nest chamber leaves the problem of breeding in E.g. namibensis still largely unsolved. European and American talpids (Dubost, 1966; Hickman, 1984a; Yates & Pederson, 1982) and African chrysochlorids (Kingdon, 1974; Kuyper, 1985) have one to several nest chambers lined with shredded grass and/or dry leaves located in extensive underground tunnel systems. These nests are used on a regular basis for parturition, sleep and for the rearing of young in the breeding season.

The young of *Chrysochloris asiatica* (Kingdon, 1974) and *Amblysomus hottentotus* (Kuyper, 1984) are born altricial and naked and in the case of *C. asiatica* may stay with the mother for two to three months. Presumably some form of underground nest chamber, perhaps located in the more stable sand beneath vegetation hummocks, is necessary for the rearing of young in *E.g. namibensis*. Presence of such a chamber remains to be confirmed.

In this present study, no embryos or obvious uterine scars were noted in eight females caught for the purposes of gut content analysis during February, March, April and August of 1984. Indeed the only indication of the time at which young are born in *E.g. namibensis* is provided by Holm (1969) who recorded two gravid females each with a single, near full-term foetus taken in October. These findings are indicative of a circumscribed seasonal breeding season in *E. g. namibensis* as has been reported by Van der Horst (1946), for the closely related *E.g. granti* collected from Port Nolloth, which has a breeding season lasting from October to November.

Movement Patterns

The movements made by a mole within its range are most likely to be determined by the distribution of food and interactions with conspecifics, particularly in the mating season.

Unfortunately, movements motivated by the search for mates and its influence on the patterns of displacement could not be defined on the basis of the collected data.

The apparent tendency for E.g. namibensis to utilise their home range in a somewhat circumscribed but 'nomadic' fashion is believed to primarily reflect foraging considerations. Namib moles feed predominantly on non-vagile invertebrate prey such as termites and insect larvae (Chap. 2). These food resources are sparse and patchily distributed in the dunes at Gobabeb and moles must therefore travel considerable distances (up to 600m a night) to fulfil their dietary needs (Chap. 2). Rather than traverse the full extent of their ranges to return to a central nest site after each foraging foray, as for example do some species of desert rodents who store or consume food in their burrows (Shroder, 1979), it is more energetically expedient for moles to conserve energy by the use of temporary rest sites. Similar behaviour has been reported for hedgehogs (Boitani & Reggiani, 1984) in the Mediterranean maquis where these insectivores must travel extensively in order to meet their food requirements.

The amount of time moles take to patrol their entire range is not known, but must take several days, since most tracks monitored for three consecutive days were not observed to cover areas previously foraged. Work on the foraging behaviour of Namib moles (Chap. 2) suggests that moles utilise their home range in such a way, that the return time to any particular area of the range has evolved as a balance between allowing resources (emerging or reproducing insects) to renew and preventing loss to other moles.

Territoriality

Construction, maintenance and modification of burrow systems by subterranean species entails considerable energetic investment (Vleck, 1981). Such species must thus place greater investment into areas they inhabit than do surface dwellers, and consequently may strongly resist displacement (Giger, 1973). Solitary habits and aggressive behaviour of many subterranean species are believed to be manifestations of intense efforts to retain home sites. Thus it is not surprising to find that home ranges of these animals are generally also their exclusive and defended territories, except for brief periods during the breeding season when multiple occupancies by both sexes occur (Nevo, 1979). This pattern is found in insectivorous moles (Arlton, 1936; Giger, 1973; Godfrey & Crowcroft, 1960; Kuyper, 1985) and rodent moles (Millar, 1964; Nevo, 1961; Reichman, Whitham & Ruffner, 1982), although sociality does occasionally occur in subterranean herbivores as exemplified by *Heterocephalus glaber* (Jarvis, 1978), *Cryptomys hottentotus* (McConnell, 1986), and *C. damarensis* (Bennett & Jarvis, 1988).

Namib moles are solitary and confine themselves to relatively constant home ranges to which they show a strong fidelity, but not necessarily spatial exclusivity as demonstrated by the varying degrees of range overlap between neighbours. Overlapping of home ranges implies lack of territoriality at least in the conventional sense of 'an exclusively defended area' (Brown & Orians, 1970; Burt, 1943). However Kaufman (1983) has expanded this earlier definition to include 'a fixed portion of an individual's or group's range in which it has priority of access to one or more critical resources over others who have priority elsewhere or at another time. This priority of access must be achieved through social interaction'. This definition differs from most others (see Kaufman, 1983 for review) in its explicit recognition of time as a territorial parameter, its rejection of exclusivity and overt defense as necessary components of territorial behaviour, and finally its inclusion of areas of exclusive use maintained by mutual avoidance.

Movements of a population of moles monitored at the Gobabeb study site over three consecutive days showed discrete centres of activity for each individual with little evidence of any direct encounters with neighbouring conspecifics. Since these observations were conducted on unidentified animals, the home range area for each was unknown, as well as the proportion of the home range utilised in the three day observation period. Nevertheless, the data are considered sufficient to demonstrate territoriality in *E.g. namibensis* as specified by Kaufman's (1983) definition, which incorporates areas of exclusive use within an animal's home range, even though such areas may be somewhat temporary in nature.

It is proposed that Namib moles have overlapping home ranges that may be too large for effective energy efficient exclusion of intruders. Each mole forages in a different area of its home range each day. These daily foraging areas might be regarded as one day territories since a definite geographical area is involved rather than a moving resource (Kaufman, 1983). It is suggested that the possibility of encounters with neighbouring animals is reduced by the implementation of some form of mutual avoidance behaviour, since no evidence of direct aggressive confrontations in the field was found. Fighting has, however, been observed in the laboratory between males, males and females on occasion, but never between females.

Mutual avoidance is known to play an important role in many mammalian territorial systems and has been demonstrated previously in such species as domestic cats (Leyhausen, 1971), hedgehogs (Boitani & Reggiani, 1984; Reeve 1982), desmans (Stone, 1985; Stone & Gorman, 1986) and primates (Waser, 1976).

For a system of mutual avoidance to operate successfully, it is necessary for an individual to recognise its immediate neighbours so that it can organise its routine activites and minimise contact with them. In the Pyrenean desman (Galemys pyrenaicus), range demarcation is effected by the continual renewal of scent marks, both faecal and from the sebaceous sub-caudal gland (Stone, 1985), while in Talpa europaea, burrows are marked regularly by the inhabitant through micturition, thereby controlling trespass (Mellanby, 1966). When the tunnels are vacated, mark effectiveness soon fails and the system is acquired by others. Some form of scent marking may occur in E.g. namibensis, possibly at rest sites underneath plant hummocks, since shifting sand does not provide a good substrate for scent deposition. However, scent marking in Namib moles, as in other chrysochlorid species has yet to be demonstrated positively in captivity or in the wild. Hickman (in press) suggested that in chrysochlorids, inadvertent communication through digging activities may result in a 'sphere of influence' in surrounding areas of burrows. In E.g. namibensis, a large malleus indicates good sensitivity to vibrations (Nolte, 1968) and possibly an ability to detect other moles in the near vicinity during surface foraging activities.

CONCLUSIONS

Examining population density, home range dynamics and movement patterns, the hypothesis emerges that the Namib dune environment does not provide enough resources to support a high population density of moles, to the extent that they must employ large home range areas in meeting their energy requirements. Furthermore, sparse and widely dispersed food resources require moles to utilise their home range in a nomadic fashion rather than continual return to a central nest area. Like other subterranean insectivores, Namib moles are largely solitary in nature and exhibit a strong home range fidelity, although there is evidence of overlap in the ranges of neighbouring animals. However, mutual avoidance, perhaps facilitated by employment of scent marks or inadvertent communication during foraging activities, appears to play an important role in reducing the frequency of encounters as observed in the natural situation.

CHAPTER 4

ACTIVITY PHASING

INTRODUCTION

When considering the relationship between an animal and its environment, no description of where an animal lives or what it does can be complete without considering when the activity takes place (Enright, 1970). Indeed morphological, physiological and behavioural adaptations which permit an organism to function efficiently in its natural habitat all relate to the time structure of the environment.

Cloudsley-Thompson (1960) has pointed out that selection pressure naturally favours organisms capable of adapting their behavioural rhythms to the periodicity of their surroundings. Subterrranean mammals spending most of their existence in closed burrow systems are subject to continual darkness and relatively constant temperature and humidity (Dubost, 1966; Kennerly, 1964). Under these conditions of minimal environmental fluctuation, it is unlikely that activity phasing is directly influenced by environmental factors, but instead is governed primarily by metabolic demands (Gettinger, 1984a; Godfrey, 1955; Vaughan & Hansen, 1961). Not surprisingly, subterranean species with few exceptions, are active both day and night (Nevo, 1979).

The Namib Desert golden mole (<u>Eremitalpa</u> <u>granti</u> <u>namibensis</u>) is a small arid dwelling chrysochlorid. An inhabitant of a sand dune environment, this species has diverged from the subterranean habits typical of most other chrysochlorids by having extensive aboveground activity and lack of a permanent underground burrow system. Factors influencing activity rhythms in surface foraging Namib moles can therefore be expected to differ from those of other subterranean mammals which spend virtually their entire lives underground.

In this present study, activity patterns of _E_. _g_. _namibensis_ were examined both in the field and in the laboratory in order to gain knowledge of:

1. The activity rhythms of this species.
2. The nature of the ecological advantage conferred by these rhythms.
3. Factors governing these rhythms.

MATERIALS AND METHODS

Field Studies

Observations in the field were conducted at a site approximately 8km from Gobabeb in the Namib dunes. Location of animals in the field (between 08h00-10h00) was determined by following surface tracks to their termination and then marking the site where animals were buried with a thin wire stake (1.5m high), and red reflective tape to facilitate observation during the night. Beginning at 18h00, marked sites were visited every hour until commencement of activity, and thereafter every two to three hours for 24 hours. New marker stakes were erected if the mole had moved from its original position, as indicated by the presence of fresh surface or subsurface tracks, and the animal scored as active for the entire one to three hour time period. This method of scoring undoubtedly underestimated the time spent in rest and overestimated the time spent in activity, but did give an approximate indication of the times of activity over the 24 hour observation period. More frequent checks of mole movement were not undertaken so as to minimise the disturbance to the animals. Distance moved (m) by each animal between marker stakes indicated amount of locomotory activity, although particular activities such as grooming which did not involve gross positional changes, were hard to detect and not recorded.

Location and tracking of wild moles were accomplished in seven 24 hour observation periods at one to two monthly intervals from September 1983 to July 1984. A maximum of four moles was monitored in any one 24 hour session, since it was difficult to follow more animals concurrently, especially during hours of darkness. During activity studies, sand surface temperatures were recorded at the study site with a data logger (Campbell CR-21) equipped with one thermistor probe accurate to 0.01°C positioned on level sand on an east facing upper dune slope approximately 2m distant from the nearest vegetation.

Laboratory Observations

Four adult males (mean mass 28.0g; S.D.±6.7) and eight adult females (mean mass 23.1g; S.D.±3.6) were collected during

1985 to 1987 and maintained in the laboratory from three months to two years. Activity patterns were recorded by a monitor housed in a constant environment room. A detailed description of the structural components and mode of operation of the activity monitor has been given by Perrin (1981). Briefly, the apparatus comprised a main console for data processing and an arena in which monitoring occurred. The arena consisted of a raised square aluminium floor (1.5m x 1.5m), walled (to 25cm) on all sides and covered with a layer of Namib dune sand (to 1.5cm). Two circular holes were positioned in the floor of two diagonally facing corners. Each hole permitted the test animal access to a glass jar (2.2ℓ) filled with sand situated directly below the main arena floor (Fig. 4.1).

The main arena walls accommodated a series of photodiodes and phototransistors positioned 25mm above the arena wall to emit and receive infra-red light beams. Five beams ran in a parallel direction across the arena, transected by five beams running in the opposite direction, forming 36 equally sized squares (Fig. 4.1). Bisection of the infra-red light beam grid due to movement of the arena occupant was automatically recorded and processed by a microprocessor based computer (C.D.P. 1802) housed in the console. Every 20 minutes an accumulated activity count (i.e. total number of light beams broken in 20 minutes) was printed on a revolving drum printer also housed within the console. Days were thus subdivided into 72 20-minute periods; an animal was considered active for

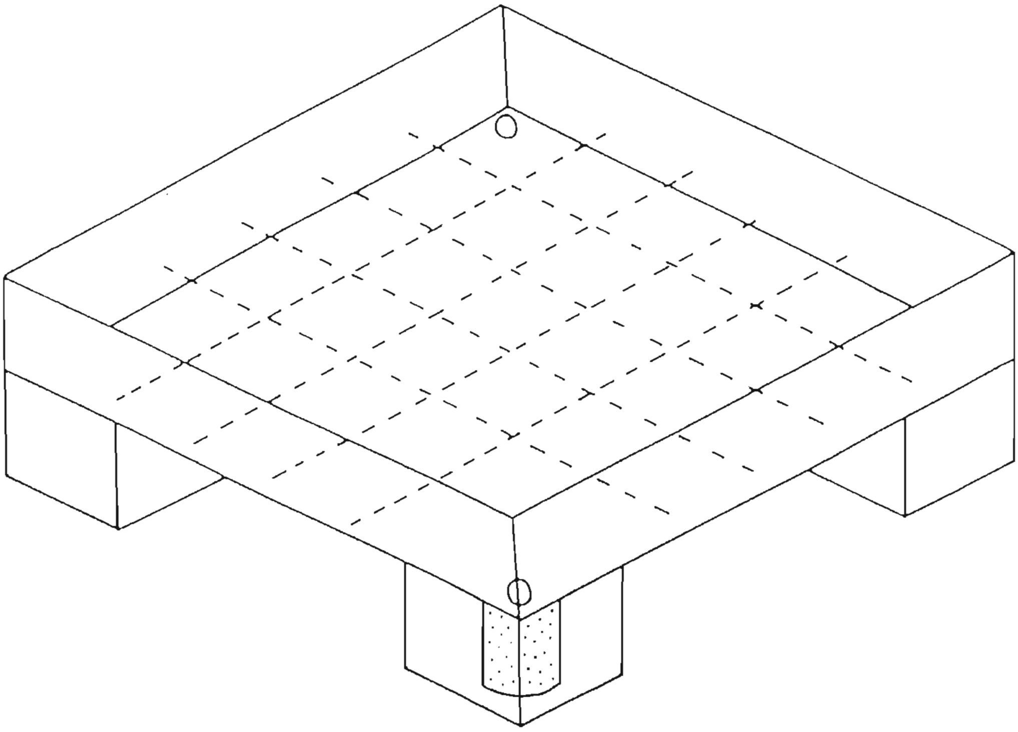


FIGURE 4.1: A diagrammatic representation of main activity arena and four lower supports, two of which house a sand filled glass jar (stippled area). Circles represent access points to sand jars from the arena and dashed lines represent the paths of intersecting infra-red light beams. Modified from Perrin (1981).

the entire 20 minute period regardless of the number of light beam crossings recorded.

The apparatus allowed for the monitoring of surface locomotory activity only. Any subterranean movement within the sandjars was not recorded.

Moles placed in the activity monitor were allowed 24 hours to acclimate before monitoring began. Light regime, temperature, food supply and monitoring period varied between different experiments, and are summarised in Table 4.1. Treatments 1-4 measured the effect of temperature and food availability on mole activity, while treatments 5-6 investigated the endogenous component of rhythmicity.

Mealworms (Tenebrio molitor larvae) were supplied to moles with an automatically timed food dispenser (Plate 4.1) which released larvae into the activity arena at approximately three hourly intervals, thus precluding any activity associated with habituation to single daily feeding times as has been reported for the Pyrenean desman (Richard, 1985) and the short-tailed shrew (Mann & Stinson, 1957). Moles were weighed prior to testing, and the sand in the apparatus sieved to remove excretory residues and any unconsumed mealworms from the previous occupant.

Immediately on removal of moles from the test apparatus (usually between 09h00-10h00), body temperature was measured by inserting a sheathed type 'K' thermocouple 5mm into the

TABLE 4.1: Experimental conditions for the monitoring of activity in *E.g. namibensis*

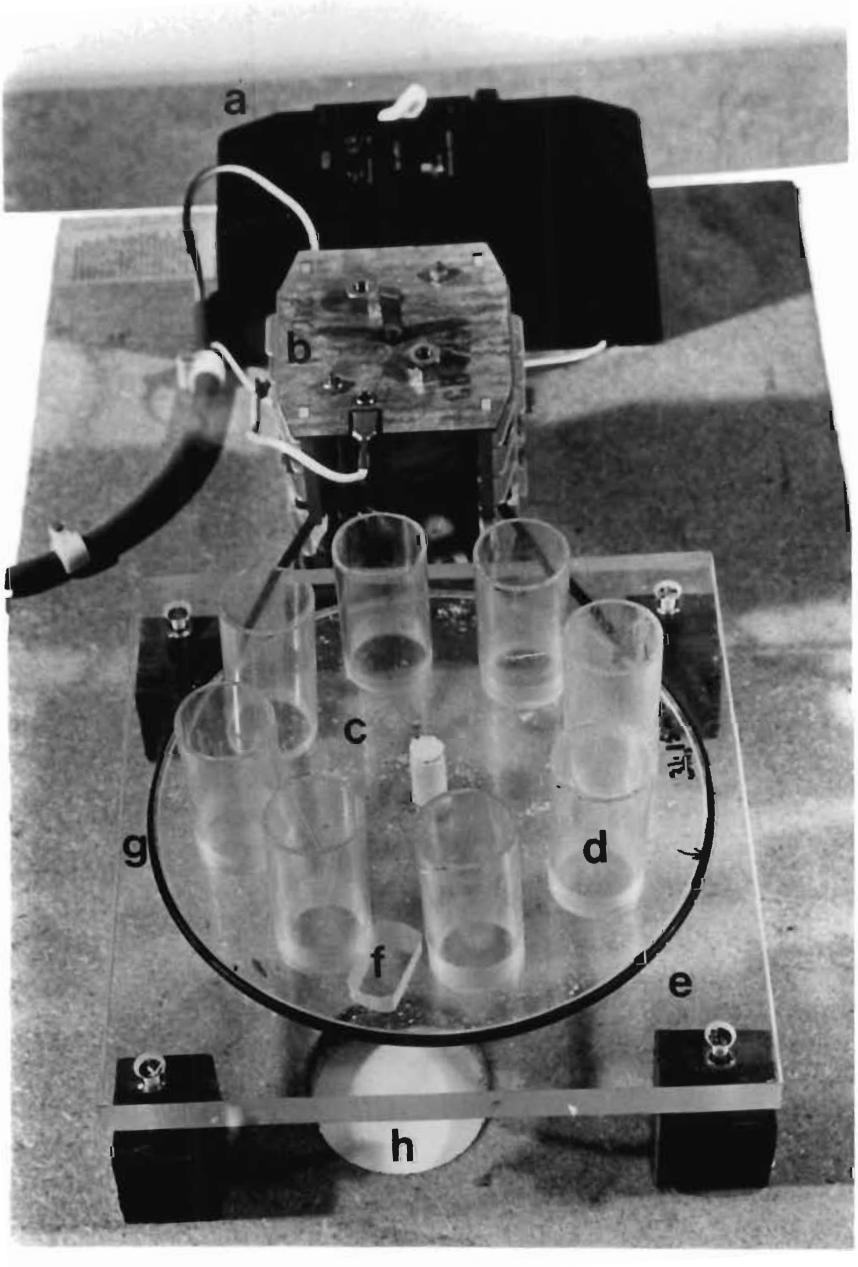
Treatment	Photoperiod (lights on)[a]	Temperature (°C)	Food supply	Monitoring period(days)	Sample size
1	07h - 19h	30	*ad lib.*[b]	2	6F, 3M
2	07h - 19h	20	*ad lib.*	2	6F, 2M
3	07h - 19h	25	*ad lib.*	2	7F, 2M
4	07h - 19h	25	*restricted*[c]	2	4F, 3M
5	-	28	*ad lib.*	9	IF
6	07h - 19h	28	*ad lib.*	9	IF

[a] Two 40w daylight-white fluorescent lights

[b] 40-50 mealworms day-1

[c] 10 mealworms day-1

PLATE 4.1: The components of an automatically timed food dispenser: a time switch with a circuit breaker (a); an electrically driven geared motor (b); a perspex distributor disk (c) into which was inserted eight vials (d) for holding mealworms, each with a 25mm hole at the bottom. The disk was mounted on a square perspex slab (e) equipped with a single aperture (25 x 15mm) (f) and was driven by means of a rubber belt (g) from the geared motor. When operating, the motor slowly revolved the disk at a rate of one revolution every 24 hours. As the vials moved over the aperture (one vial every three hours) mealworms were released and fell through a circular hole (h) in the chipboard mounting block (i) onto the floor of the activity monitor arena.


a
b
c
d
e
f
g
h

cloaca. The thermocouple was attached to a Digitron 1408 thermometer accurate to ±0.01°C.

RESULTS

Activity in the Field

A total of 25 moles were located for the seven 24 hour observation periods conducted in the field. Of these animals, six were 'lost' due to tracking errors, while 19 were followed successfully. Only these 19 moles were considered for the analysis of activity and were divided into two relatively homogeneous seasonal groups (Table 4.2).

Daily activity profiles

Namib moles have a distinct nocturnal pattern of locomotory activity, although occasional periods of daytime activity both in the morning and the afternoon were evident for some individuals (Fig. 4.2). This nocturnal rhythmicity was reflected in the percentage of day to night activity, with all moles being more active in darkness than during daylight hours (Table 4.2). Daytime activity always took the form of subsurface sandswimming while surface locomotion was prevalent at night. During winter months, commencement of the nighttime active phase began shortly after sunset, but in summer a trend towards delayed emergence was noted (Fig. 4.2).

Seasonal activity profiles

The total daily activity (t.d.a.) (Table 4.2) for animals in summer and winter showed no significant seasonal variation (Student's t-test: $t=1.99$; $p>0.05$; d.f.=17). However, mean

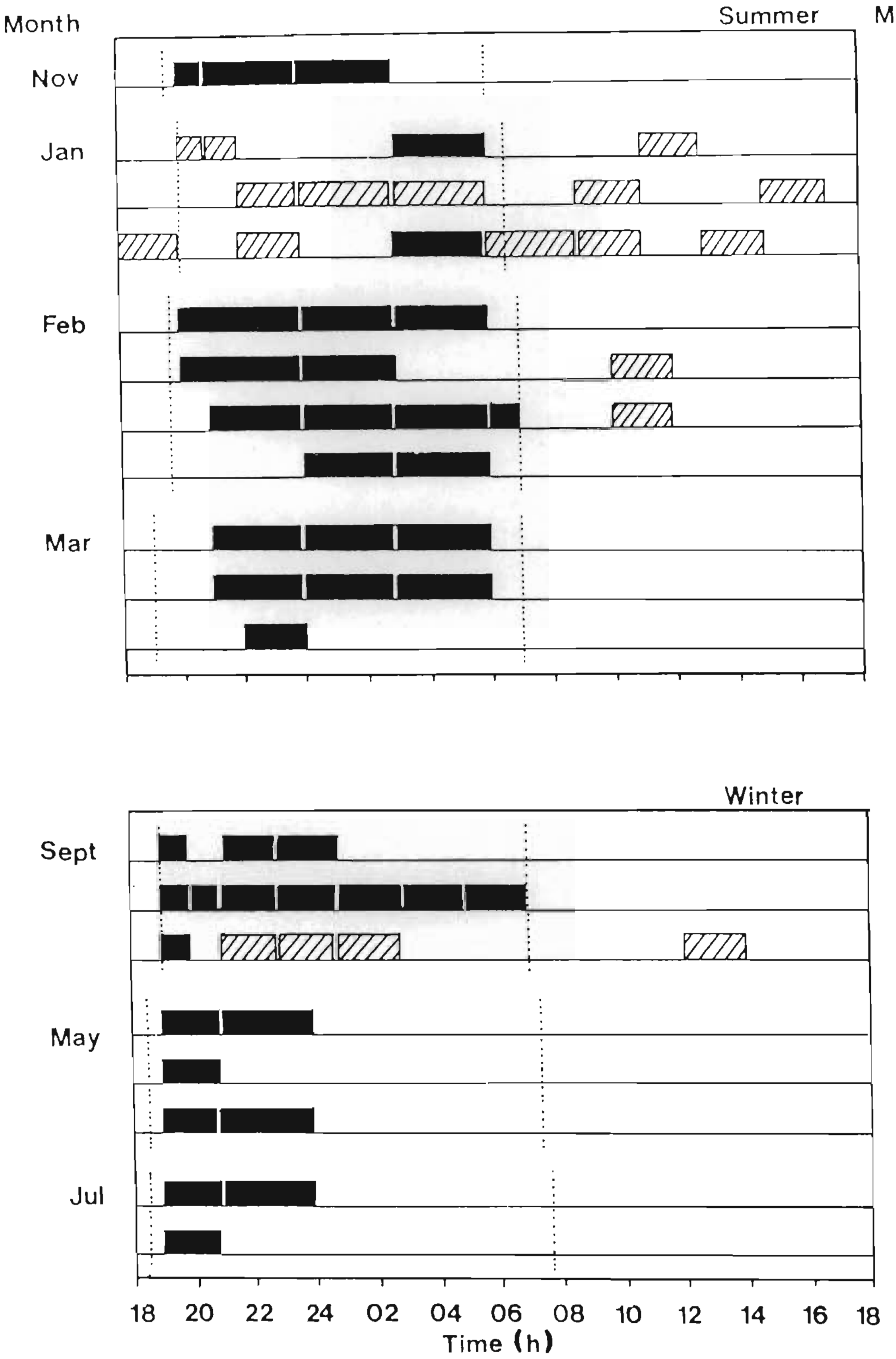


FIGURE 4.2: Activity patterns obtained for E.g. namibensis in the field. Blocks indicate one-three hour time periods in which movement recorded (solid- surface movement, hatched- sandswimming), dotted lines represent sunrise and sunset.

activity profiles established for the two seasonal groups indicate a clear seasonal trend in the temporal organisation of activity (Table 4.3). In winter, the percentage of activity occurring between sunset and midnight was significantly greater than in all other time periods, while in summer, level of activity between sunset and midnight was not statistically distinguishable from that between midnight and sunrise.

Surface temperature and mole activity

The timing of mole activity in relation to thermal conditions on the sand surface (Fig. 4.3) showed, that while sandswimming was independent of surface conditions, surface locomotion was restricted to a circumscribed temperature range. Mean temperature at which onset of surface activity occurred did not differ significantly (Student's t-test: $t=0.32$; $p>0.05$; d.f.=16) between summer ($\bar{x}=24.7^{\circ}C$) and winter ($\bar{x}=25.1^{\circ}C$), although sand surface temperatures at sunset in summer ($\bar{x}=31.6^{\circ}C$) were higher than those in winter ($\bar{x}=25.3^{\circ}C$). Similarly, temperature at which cessation of surface activity occurred in winter ($\bar{x}=16.0^{\circ}C$) did not differ significantly (Student's t-test: $t=0.85$; $p>0.05$; d.f.=16) from that in summer ($\bar{x}=17.2^{\circ}C$), although temperature minima in winter ($\bar{x}=11.3^{\circ}C$) were considerably lower than those in summer ($\bar{x}=16.5^{\circ}C$).

TABLE 4.3: Comparison of percentage activity in *E.g. namibensis* at different times of day in summer and winter. Values expressed as the mean ±1 S.D.

Time period	% activity[a] Winter (n=8)		Summer (n=11)	
Sunset - midnight	89.2 ± 14.0		43.4 ± 30.3	b
Midnight - sunrise	8.1 ± 12.4	b	50.4 ± 31.6	
Sunrise - midday	1.0 ± 2.7		3.4 ± 6.1	b
Midday - sunset	1.6 ± 4.3		3.0 ± 4.6	
Results of one-way anova (after arc-sin) transformation	F=2.95; d.f.=3.28 $p<0.001$		F=2.84; d.f.=3.40 $p<0.001$	

[a] % activity calculated as $\frac{\text{distance moved in time period}}{\text{Total distance moved in 24 hours}} \times 100$

[b] Vertical lines indicate no significant difference between time periods (Student-Newman-Keuls multiple range test)

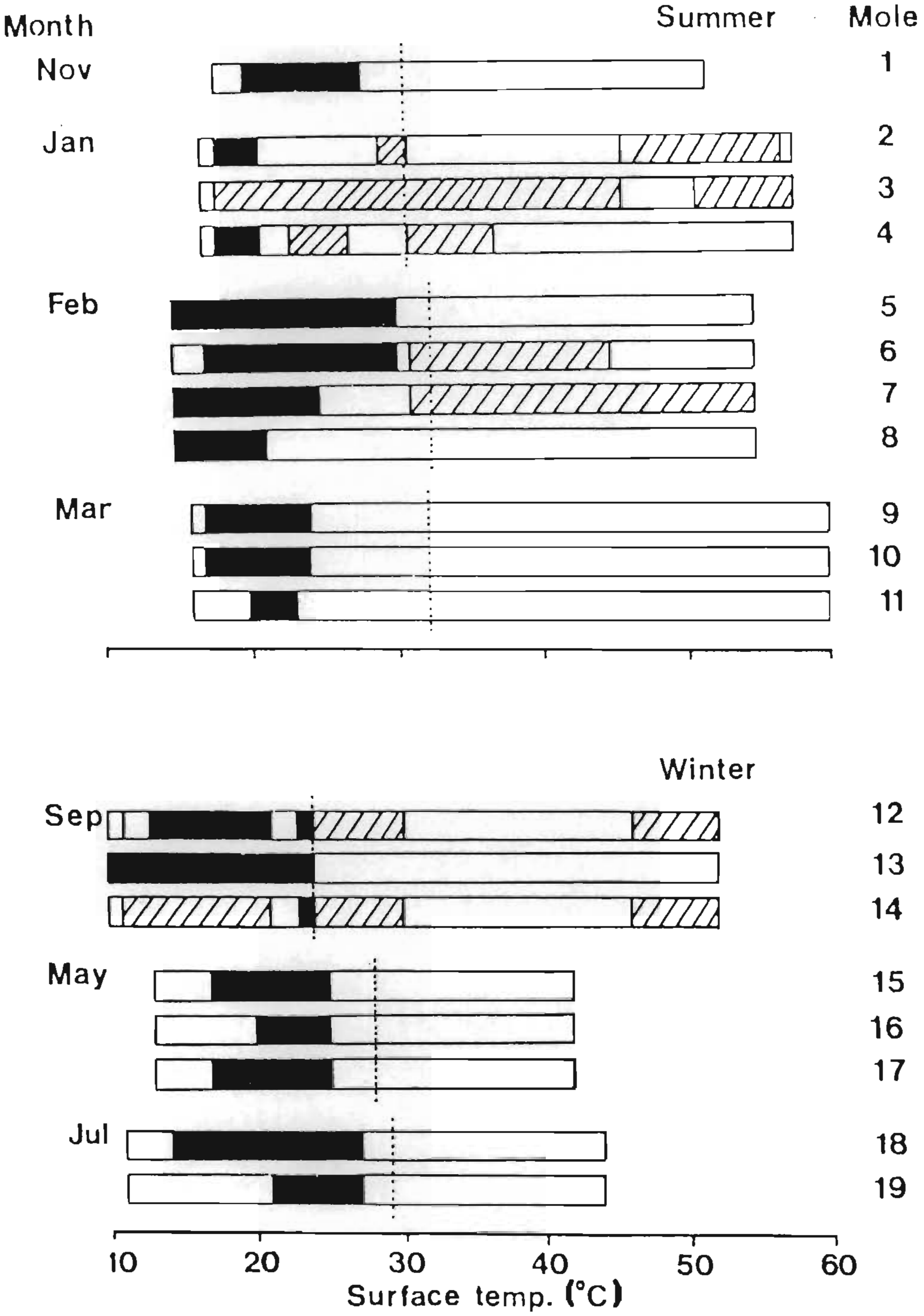


FIGURE 4.3: Sand surface temperature and mole activity. Rectangles enclose minimum and maximum temperature, blocks indicate temperature range over which activity occurred (solid-surface movement, hatched-sandswimming), dotted lines give surface temperature at sunset.

Activity under Laboratory Conditions

Effect of temperature and food availability (Treatments 1-4)

A basic 24 hour rhythm of locomotory activity was apparent for _E.g._ _namibensis_, with individuals showing one to two major periods of activity per day. The intensity and temporal sequence of activity was characterised by great intrapopulation variance.

Firstly there were marked differences between individuals in activity profiles (number of light beams broken per hour). Figs. 4.4a and 4.4b illustrate the difference in the intensity and temporal sequence of activity in two males, each recorded over two days at 25^{o}C with food supplied _ad lib_.. Animal 1, with a high activity score, exhibited two daily periods of activity, one in the afternoon followed by a major nocturnal period, while animal 2, characterised by a low intensity of activity, was exclusively nocturnal.

Secondly there was variation within-individual activity profiles in:

1. The timing of activity bouts as exemplified by a single male at 25^{o}C on a restricted food supply (Fig. 4.4c; animal 3), where the temporal sequence, but not intensity, of activity periods varied over the two day recording period. On the first day there were two activity periods, one diurnal and one nocturnal while on the second day, activity was exclusively nocturnal.

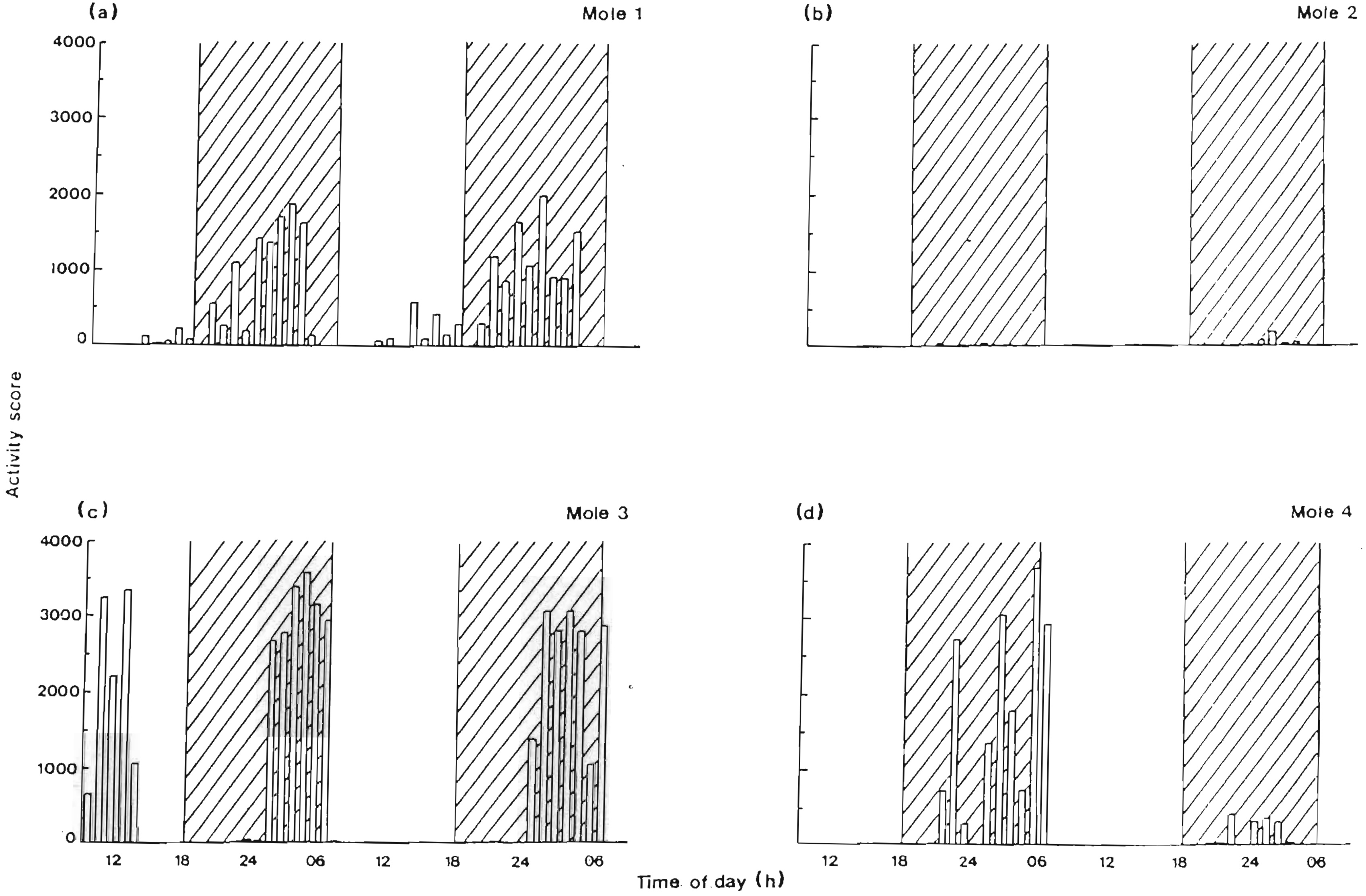


FIGURE 4.4: Individual activity profiles of *E.g. namibensis* to show intrapopulation variance in the intensity and temporal sequence of activity. Activity score = number of light beams broken hour^{-1}, hatched areas indicate periods of darkness.

2. The intensity of activity as typified by a single male at 30°C (food supplied _ad lib._) which showed an attenuation in activity scores on successive days, although the temporal sequence remained the same (Fig.4.4d; animal 4).

In spite of the large intrapopulation variance, composite profiles (plotted using the means of activity counts) demonstrate clear differences both in the intensity and temporal pattern of activity between treatments (Fig. 4.5). For animals at 30°C and at 25°C with food restricted, the emphasis was on nocturnal activity, while animals at 25°C and 20°C with food provided _ad lib._ tended towards bimodality, with both nocturnal and diurnal activity peaks. To facilitate quantitative comparisons between activity profiles, four activity variables were defined after Nevo, Guttman, Haber and Erez (1982):

1. Summation/intensity of activity: Total number of activity pulses (i.e. light beams broken) during 24 hours.
2. Duration of activity: The percentage of 20-minute time units during 24 hours in which at least one pulse of activity was recorded.
3. Number of activity bouts: The total number of continuous bouts of activity during the 24 hours. An activity bout is defined as the time duration in which at least one pulse was recorded in each 20-minute unit.
4. Length of activity bouts: The total time duration of sequential 20-minute units in which at least one pulse

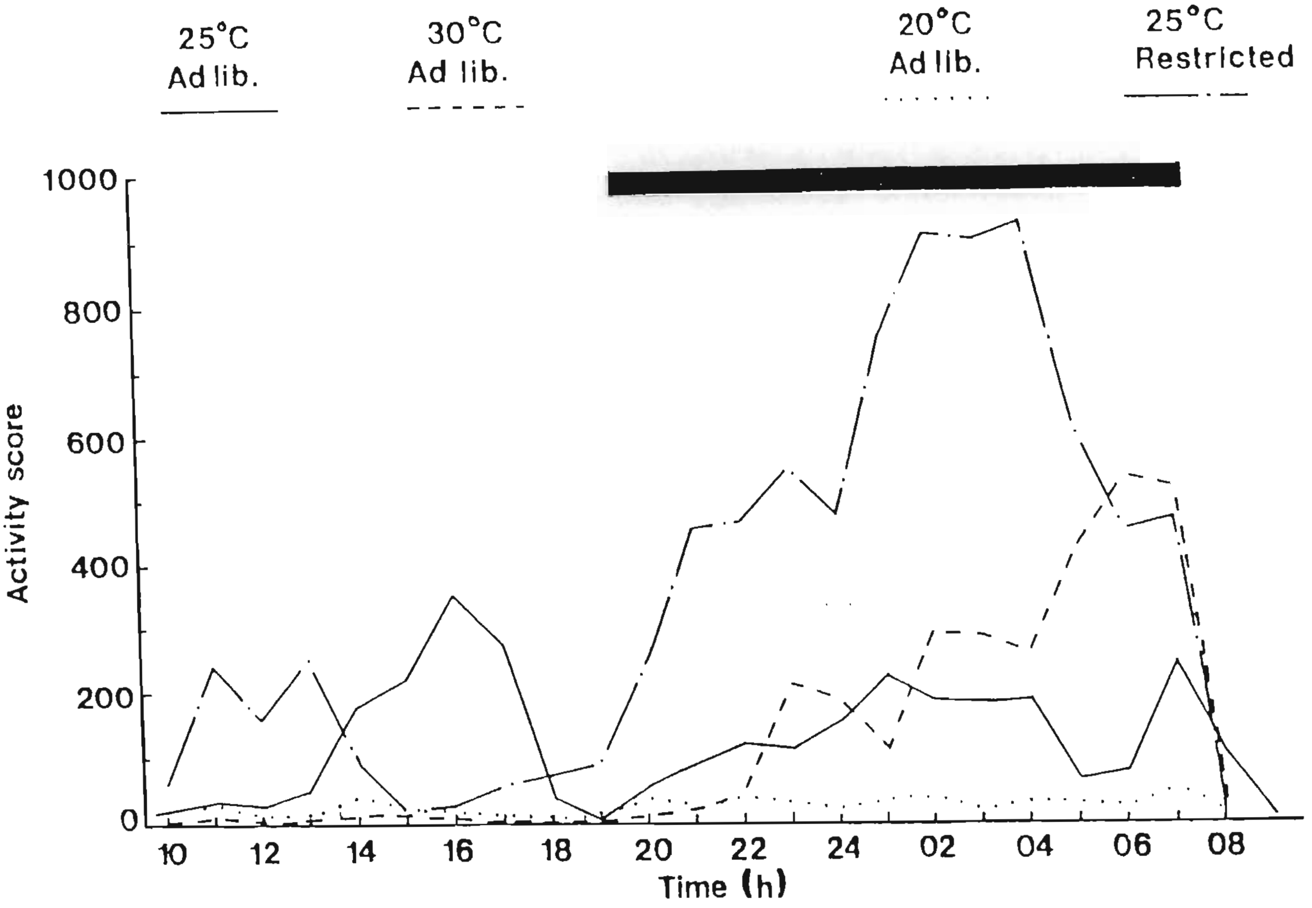


FIGURE 4.5: Composite activity profiles of E.g. namibensis subject to different temperature and feeding regimes. Activity score = mean number of light beams broken $hour^{-1}$, solid bar indicates period of darkness.

was recorded.

Differences in activity variables between treatments are summarised in Table 4.4, refer also to Fig. 4.5. Mean values reported for summation of activity and length of activity periods are somewhat misleading because of great variation between individuals as indicated by large standard deviations. This variation greatly influenced mean values, but did not seriously affect mean ranking which was tested by the Kruskal-Wallace test.

Animals with restricted food exhibited significantly higher activity levels than all other treatments with food supplied *ad lib*.. Also, a clear trend for reduced intensity of activity with decreasing temperature was evident, paralleled by a decrease in body temperature of experimental animals. Duration of activity was similar for all treatments, although differences were observed for the number of activity bouts. Significantly fewer activity bouts occurred when food was restricted. Absolute durations of individual periods of activity were extremely variable with 40-50% of all bouts lasting 20 minutes or less (Fig. 4.6). All treatments, however, included at least one activity bout of longer than four hours duration; the longest period recorded was 12 hours for a male specimen under conditions of restricted food. Overall, activity bouts for food restricted animals were of longer duration than those for animals with *ad lib*. food treatments subject to different temperatures (Table 4.4).

TABLE 4.4: Comparison of four activity variables and body temperatue of E.g.namibensis subject to different temperature and feeding regimes. Values expressed as the mean ±1 S.D.

Treatment		No. of animals	No. of pulses/day		%activity/day	No. of activity bouts/day		Length of activity bouts (mins)		Body Temperature (°C)	
Food *ad lib.*	30°C	9	2718± 717	a	26.6± 8.1	7.6±3.1	b	54.0 ± 26.0	a	33.6±0.6	
	25°C	9	2318±3965		30.3±17.5	7.4±3.1		60.0 ± 84.9		29.8±1.5	
	20°C	8	476± 536		27.4±14.8	8.8±3.7		46.2 ± 60.4		26.7±3.8	b
Food restricted	25°C	7	8239±7952		35.5±16.9	4.5±1.3		120.9 ±167.9		29.2±1.8	
Results of one-way anova or Kruskal-Wallace test			H=14.91; d.f.=3 $p<0.05$		F=1.18; d.f.=3,62 N.S.	F=5.33; d.f.=3,62[c] $p<0.005$		H=8.69; d.f.=3 $p<0.05$		F=13.44; d.f.=3,26 $p<0.0005$	

Vertical lines indicate no significant difference between treatments tested using

[a] Non-parametric multiple comparison tests

[b] Student-Newman-Keuls multiple range test

[c] After arc-sin transformation

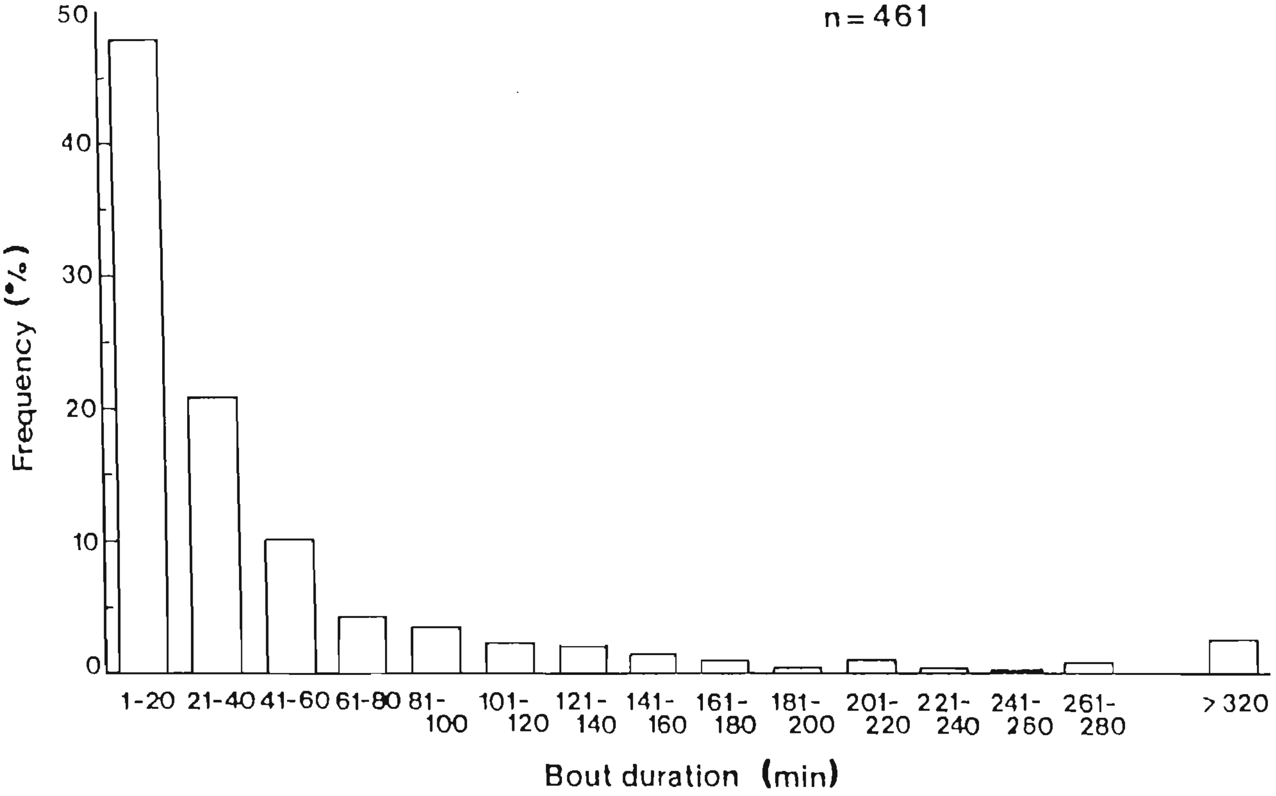


FIGURE 4.6: Frequency distribution of the duration of bouts of activity for _E.g._ _namibensis_.

To summarise:

1. Animals with restricted food exhibited a higher intensity of activity with fewer but more extended activity bouts than animals with *ad lib*. food.
2. Differences in temperature altered intensity of activity, but did not affect duration of activity, nor the number and length of activity bouts.

Day and nighttime activity

Differences in the day/night intensity and duration of activity for each experimental treatment are summarised in Table 4.5, again refer to Fig. 4.5.

The percentage of nocturnal activity was similar for all treatments and greatly exceeded that during the day. However, intensity of daytime activity relative to that at night increased with decreasing temperatures until at 20°C no significant difference between light and dark activity levels was observed. Animals with restricted food at 25°C exhibited a similar daytime intensity of activity to those at 25°C with food supplied *ad lib*., but showed much higher levels of activity at night.

Day and nighttime differences in number and length of activity bouts were not examined, since in many instances, activity bouts initiated during the day extended into the dark phase and vice-versa. This made classification of activity bouts as either in light or dark periods difficult.

TABLE 4.5: Differences in day/night activity of *E.g. namibensis* subject to different temperature and feeding regimes
Values expressed as the mean ± 1 S.D.

Treatment		No. of animals	No. of pulses Day	Night	Significance[b]	% activity[a] Day	Night	Significance[c]
Food *ad lib*.	30°C	9	75.6 ± 117.1	2705.5±4727.9	$p<0.001$	25.9±21.9	73.5±23.2	$p<0.001$
	25°C	9	1268.0 ±2816.3	1661.1±3260.4	$p<0.02$	35.5±17.8	65.1±18.1	$p<0.005$
	20°C	8	167.1 ± 418.0	307.7± 404.8	N.S.	28.9±21.3	71.7±21.1	$p<0.005$
Food restricted	25°C	7	1076.4 ±2785.0	7162.5±6050.0	$p<0.001$	27.8±20.9	72.2±20.7	$p<0.002$

---

[a] % day/night activity calculated as $\frac{\text{No. of 20-minute units in which activity recorded during day/night}}{\text{Total no. of 20-minute units in which activity recorded during 24 hours}} \times 100$

[b] Wilcoxon paired sample test

[c] Paired sample t-test (after arc-sin transformation)

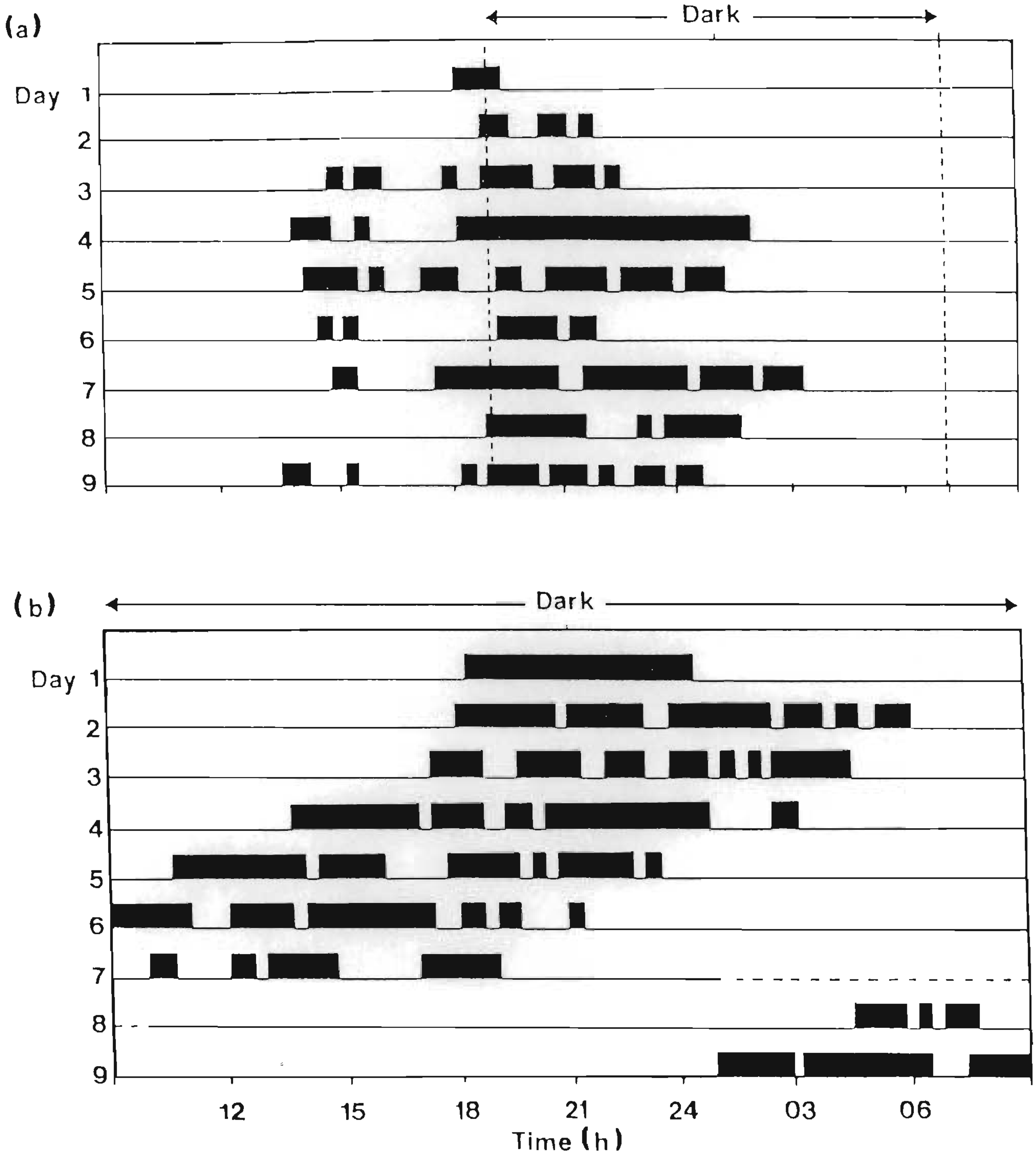


FIGURE 4.7: Times of activity (darkened blocks) for a single female E.g. namibensis exposed to (a) 12 hour light cycle and (b) continuous darkness. Broken horizontal line (day 7-8 in b) indicates malfunctioning of activity monitor during which time no data were collected.

Activity rhythms in the absence of light

A single female mole exposed to a normal light cycle (light during 07h00-19h00) for nine consecutive days, exhibited a clear unimodal pattern of activity consisting of several activity bouts of variable length which occurred between 14h00-02h00 (Fig. 4.7a).

This unimodal pattern of activity was retained during a nine day period in continuous darkness (Fig. 4.7b). However, onset of activity fell at an earlier time each day. This was brought about by a shortening of the 24 hour cycle by between 20-220 minutes each day while in continuous darkness. The onset of activity which occurred at 18h00 on the first day had shifted back to 24h40 by the ninth day.

DISCUSSION

Previous reports, based largely on incidental laboratory observations, are not unanimous regarding the diel periodicity of E.g. namibensis. Meester (1964) reported that captive Namib moles were active at intervals throughout the day and night with a main period of activity at midday, while Nolte (1968) found main activity periods occurring during midmorning and late afternoon. In contrast, Holm (1969) described strictly nocturnal activity both in the laboratory and the field. Such conflicting reports are not surprising considering the findings of this present study: the basic temporal pattern of locomotory activity in E. g. namibensis under natural conditions was almost exclusively nocturnal, but captive moles exhibited considerable lability in their daily rhythmicity in response to different experimental conditions.

Information concerning biological rhythms gained from observations of animals under captive conditions has often been criticised, since such observations necessarily preclude the influence of a multiplicity of environmental factors that are major determinants of activity patterns in the field (Ashby, 1972; Genoud & Vogel, 1981; Kavanau, 1969; Stone, 1987). This criticism may well be valid in situations where laboratory observations are the exclusive source of information on aspects of rhythmicity. Nevertheless, laboratory experiments conducted under controlled conditions, and performed in conjunction with field observations (as in this present study), can provide a good indication of the environmental variables responsible for the inhibition and promotion of locomotory activity.

What, then, are the primary determinants of nocturnal activity in E.g. namibensis in their natural environment?

Avoidance of Extreme Conditions

Arid dwelling subterranean mammals, afforded protection from thermal extremes and desiccating conditions by their burrow systems, do not display obvious patterns of temperature selection or avoidance, with activity periods encompassing both daily extremes of temperatures, as for example in the pocket gopher (Thomomys bottae) (Gettinger, 1984a), and the mole rat (Spalax ehrenbergi) (Nevo et al., 1982). In other small desert inhabiting mammals, nocturnalism is most often associated with avoidance of high temperatures and the need to conserve water (MacMillen, 1972; Morton, 1980). Similarly, the Namib mole, as a surface forager, is potentially subject to rigorous diurnal conditions which pose problems with regard to heat and water balance. Maximum daily sand surface temperatures measured during the present study ranged from 42-59°C, which is well beyond the thermoregulatory capabilities of E. g. namibensis (Chap. 5). However, measurements of subsurface sand temperatures in the Namib dunes (Chap.5, Fig. 5.6) have demonstrated that with increasing depth, thermal conditions within the sand column become more moderate and stable. Thus moles active during the day can easily circumvent temperature extremes by sandswimming below the sand surface. Indeed, subsurface locomotion was occasionally observed when dune surface temperatures were at their maxima (12h00-14h00).

Nevertheless, because of the sparse and patchy distribution of food resources in the Namib dune environment (Chap. 2) E. g. namibensis is, in most situations, energetically constrained to employ low cost surface locomotion in favour of the more metabolically expensive sandswimming behaviour (Vleck, 1981). Consequently, all major periods of locomotory activity in the field were restricted to night, when surface temperatures had decreased sufficiently to allow moles to forage on the sand surface. In the laboratory, on the other hand, constant and equable temperature conditions (±25°C) permitted surface activity during the day.

Many small mammals, including shrews and rodents, exhibit seasonal levels of activity which are influenced by changes in ambient temperature (Buchalczk, 1972; Churchfield, 1982; Kenagy, 1973). In this present study, moles showed no evidence of a reduced total daily activity (t.d.a.) in winter, although the seasonal proportions of the nocturnal schedule devoted to foraging are of interest. Moles during winter months usually ceased activity before midnight, but in summer months foraged throughout the night. This seasonal trend in the temporal organisation of activity can be reasonably interpreted with a knowledge of the metabolic characteristics of *E. g. namibensis* (Chap. 5). Namib moles have poor thermoregulatory abilities and are characterised by a low and labile body temperature. Consequently, activity levels (summation) were affected by even moderate temperatures, with laboratory maintained moles at 20°C exhibiting hypothermia and significantly reduced activity in comparison to animals at 30°C. Thus, in winter, generally cooler conditions prevailing during the later part of the night, in comparison to summer, may curtail surface activity, since moles are not able to maintain body temperatures within operable levels for nocturnal surface activity. Likewise, many species of heterothermic insectivorous bats hunt for shorter periods of time in cold weather and may cease foraging altogether when the temperature falls below a certain threshold (O'Farrell & Bradley, 1970; O'Shea & Vaughan, 1977). The sand surface temperature threshold below which inhibition of surface activity occurs in *E. g. namibensis* may lie close to 16°C, since this was the surface temperature at which cessation of activity usually occurred in the field.

Predator Avoidance

The extensive underground burrow systems constructed by subterranean mammals not only provide a sheltered environment, but also escape from surface predators. As Hickman (1980) has pointed out, it is unlikely that nocturnal or diurnal predators (felids, viverrids, canids, snakes and owls) exert sufficient selective pressure at different time periods to favour a night or day activity pattern in subterranean mammals.

For the few species that are surface foragers such as the chrysochlorids *Chrysospalax trevelyani* and *E. g. namibensis*, the role of predator avoidance in nocturnal behaviour patterns is questionable. Maddock and Hickman (1985) cited predator evasion together with thermoregulatory constraints as the main reasons for nocturnality in *C. trevelyani*, while Kuyper (1979) suggested that reduced nocturnal 'surface forage digging' in *Amblysommus hottentotus* may have adaptive value against nocturnal predators. However, avoidance of predators can not account for the observed activity patterns in *E. g.*

namibensis, since they are most likely subject to a wider range of predators at night than when diurnally active. Confirmed predators of E.g. namibensis include the owls Bubo africanus and Tyto alba (Nel, 1969; Skinner, Lindeque, Van Aarde & Dieckmann, 1980; Tilson & Le Roux, 1983) while Holm (1969) reported tracks of genets (Genetta genetta) and jackals (Canis mesomelas) following the trails of Namib moles, with occasional signs of digging for them. Diurnal dune predators, on the other hand are few, and in the present study included only crows (Corvus alba) and pale chanting goshawks (Melierax canorus) seen occasionally at the study site.

Diet and Prey Availability

In addition to the problems of heat, water balance and predator avoidance, a determinant of the distribution of activity of mammals between day and night, includes the problem of obtaining and assimilating adequate food. The limits this imposes on activity patterns are most restrictive in those species with high mass specific metabolic rates, and where the items of food are small, mobile and widely dispersed as in the case of many soil arthropods (Ashby, 1972). For instance, in many species of shrews, satisfaction of metabolic demands necessitates frequent foraging bouts distributed evenly through the day and night (Churchfield, 1982; Genoud, 1984; Genoud & Vogel, 1981; Mann & Stinson, 1957). Variable short rhythms consisting of three and seven activity periods per day are also characteristic of the subterranean insectivores Talpa europea (Godfrey, 1955; Meese & Cheeseman, 1969; Mellanby, 1967) and _A_. _hottentotus_ (Kuyper, 1985). These polyphasic rhythms are believed to be controlled by hunger and the need to process more food. _E_._g_. _namibensis_ feeds predominantly on termites (Chap. 2), which by virtue of their sociality together with high fat and protein content (Redford & Dorea, 1984), constitute a concentrated food source of high calorific value. The nutritional quality of such a diet coupled with very low energy requirements in Namib moles (Chap. 5) obviates the need for repetitive short-term feeding bouts spread throughout the diel cycle.

The predominantly nocturnal activity phasing in _E_._g_. _namibensis_ can be interpreted as a response to the times of food availability. The selective advantage of matching a predator's activity pattern to that of prey is obvious. Such matching considerably increases the probability that the time spent foraging will give the greatest possible energy yield with the smallest possible expenditure of energy (Erkert, 1982). For instance, many species of insectivorous bats display a strong biphasic periodicity in their activity, characterised by post-sunset and predawn peaks of activity which closely correlate with the diel abundance of aerial prey (Fenton, Boyle, Harrison & Oxley, 1977; Racey & Swift, 1985). Unfortunately, little is known of the temporal abundance of the major prey item of _E_._g_. _namibensis_, the dune termite _Psammotermes_ _allocercus_ _silvestri_. However, because of extreme diurnal conditions in the Namib dunes, there is considerably more nocturnal activity time available to ectothermic animals, and most Namib dune invertebrates occupy this temporal niche (Holm & Edney, 1973; Robinson & Seely, 1980). For the Namib mole, it would clearly be energetically inopportune to forage extensively during daylight hours by means of metabolically expensive sandswimming when prey is likely to be temporally scarce.

The motivation for occasional bouts of subsurface activity observed in the field during the day is not known, but does not appear to be associated with feeding. In the laboratory, even at an equable temperature of 25°C, the far greater proportion of night to day activity in animals with restricted food in comparison to moles with food supplied ad lib., indicated that food searching behaviour was concentrated within periods of darkness. Similar findings have been reported for the Pyrenean desman (Galemys pyrenaicus) (Stone, 1987) which forages intensively at night on stream invertebrates, but is rarely observed to feed during its shorter diurnal activity period.

In this present study, field activity patterns constructed on the basis of one to three hour intervals were an incomplete representation of the actual time course of activity. Nevertheless, continuous recordings of animals in the laboratory provided with food ad lib., revealed that the daily active phase was generally composed of many bouts of movement and pauses for rest, probably correlated with frequent excursions into the activity arena to feed. Moles on restricted rations, however, exhibited higher levels of activity and partook of fewer but more extended activity bouts. This behaviour is probably a more accurate representation of activity phasing in the field, where there is a need for continued searching for patchily distributed prey resources in an extensive sand dune ecosystem.

The Endogenous Origin of Mole Activity Rhythms and the Timing of Activity

Eremitalpa g. namibensis kept under constant conditions of darkness, humidity, temperature and food supply for nine days, maintained an activity rhythm with a roughly diurnal periodicity, although the period of this cycle deviated every day by a more or less constant amount from that of the earth's 24 hour rotation. This implies that activity rhythms in Namib moles (as in most other animals) are not induced by stimulus response systems, i. e. exogenous influences, but are based on an endogenous or circadian rhythm (Ashby, 1972; Calhoun, 1945; Dann & Slopsema, 1978; Enright, 1970). Circadian rhythms, free running under constant conditions with a period different from 24 hours, are synchronised with the external diurnal cycle by certain diurnally varying environmental factors variously termed *Zeitgebers*, synchronisers or entraining agents (Aschoff, 1960).

Entrainment of daily activity in *E.g. namibensis* (as in many mammals) is apparently caused by the periodicity of rapid changes in light intensity, i.e. dawn and dusk (Enright 1970; Nielsen, 1984). Supporting light as a *Zeitgeber* is the observation that a mole exhibiting a free running rhythm under conditions of constant darkness was entrained by a 12h:12h light dark cycle. It is suggested that changes in illumination experienced by E.g. namibensis during surface foraging activities in their natural environment acts as a trigger for the 24 hour rhythm found in these animals. Similarly, light is thought to be an important factor in the entrainment of daily activity in the mole rat (Tachyoryctes splendens) which periodically comes to the surface to forage (Jarvis, 1973). However, for the majority of subterranean mammals which seldom exit from their underground burrow systems, it is probable that conditions of constant darkness have resulted in the absence of a diel cycle governed by light (Godfrey, 1955; Hickman, 1984b; Kuyper, 1979; Vaughan & Hansen, 1961).

How Namib moles are able to perceive changes in illumination is not known, since only a vestigial eye is present which is covered with skin and fur (Gubbay, 1956; Nolte, 1968). Sweet (1909), in a study of the eye structure of the chrysochlorids A. hottentotus and Chrysochloris asiatica, concluded that both species were probably insensitive to light. In mammalian species, however, perception of changes in illumination need not occur exlusively through the eyes. Research on the blind fossorial mole rat (S. ehrenbergi) (Pevet, Kappers & Nevo, 1976; Pevet, Heth, Haim & Nevo, 1984) has indicated that the non-occular Harderian gland and pineal gland may be implicated in photoperiod perception. Further research in E.g.

namibensis must aim towards elucidating the involvement of the Harderian gland, the pineal gland and the atrophied eyes in perception of light stimuli.

Although it is generally accepted that in most animals, changes in light during the course of the day is the chief Zeitgeber that entrains circadian rhythms, diel temperature fluctuations have been shown to be important for the synchronisation of activity in some species such as the desert dune lizard (Aporosaura anchietae) (Holm, 1973) and the heterothermic insectivorous bat Molossus ater (Erkert & Rothmund, 1981).

Although the effectiveness of temperature oscillation as a Zeitgeber for mole activity was not investigated, laboratory studies did show that the circadian activity cycle of E.g. namibensis is influenced by constant low ambient temperature (25°C and below) to tend towards bimodality, with a major nocturnal peak of activity and a secondary daytime peak of activity. In contrast, moles exhibited a unimodal rhythm with emphasis on nocturnal activity at constant high ambient temperature (30°C), indicating that surface activity during daylight hours was inhibited by temperatures greater than 25°C. On the basis of these findings, it is suggested that while light may have a timing effect on the circadian rhythm of free-living Namib moles similar to that found in other animals, the effect of temperature modifies its effect on the initiation of activity, with moles regulating their emergence according to the temperature of the sand above. This explanation would account for the fact that E.g. namibensis was only seen above ground within a relatively circumscribed thermal regime with emergence onto the dune surface usually occurring at a sand surface temperature of 25°C. It would also account for the trend towards later emergence after sunset noted during summer, with onset of surface activity delayed until surface temperatures had dropped to equable levels (±25°C). In winter, however, emergence soon after sunset reflected the generally cooler conditions prevailing at nightfall.

It is not clear from the results of this study, however, whether variation in mole emergence times throughout the year simply reflected temperature selection, or alternatively a temperature induced shift in diurnal activity as Norris and Cavanau (1966) found for the sandburrowing snake (Chionactus occipitalis). These animals, like Namib moles, remain below the sand surface until sand temperature drops to a habitable level. Once the snake has emerged, the biological clock is reset allowing the animal to become active again, often somewhat less than 24 hours later, and thus to take advantage of daily thermal variation in the habitat.

Confirmation of the role of temperature as a Zeitgeber in the synchronisation of mole activity awaits experimental verification by study of the influence of temperature oscillation on entrainment of free-running circadian rhythms.

CONCLUSIONS

Daily activity rhythms in *E.g. namibensis* show adaptive variation from the polyphasic activity typical of other subterranean mammals, as a result of special ecological characteristics associated with surface activity in an energy sparse and thermally demanding sand dune habitat. Ecological advantages conferred by nocturnal activity phasing in *E.g. namibensis* relate primarily to physiological capacities for maintaining heat and water balance in an environment characterised by large diurnal temperature fluctuations, but may also involve being active at a time when availability of food is likely to be highest. Daily rhythmicity in *E.g. namibensis* is regulated by an endogenous circadian rhythm with light and possibly temperature functioning as the main *Zeitgebers* to synchronise this circadian rhythm with the periodicity of the external environment.

CHAPTER 5[1]

THERMOREGULATION

INTRODUCTION

Behavioural adaptations such as nocturnalism and burrowing habits are employed by many small mammals to avoid environmental extremes. Thus the physiological abilities of such animals are more related to selected microenvironmental conditions than prevailing climate (Buffenstein, 1984a; Bradley & Yousef, 1975). This premise is especially true of subterranean mammals which spend most of their existence in closed burrow systems where environmental fluctuation is minimal in comparison to above ground conditions (Dubost, 1968; Kennerly, 1964).

McNab (1966, 1979) concluded that subterranean mammals, although having evolved in several taxonomically diverse families, possess several similar physiological characteristics including relatively low body temperature with a tendency towards reduced thermoregulatory capacity, reduced basal metabolism and elevated thermal conductance. He proposed that these metabolic tendencies reduce overheating in burrows where evaporative and convective cooling are of little importance. Vleck (1979, 1981) and Jarvis (1978)

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[1] This chapter together with abstract and references is in press in the Journal of Arid Environments under the full title 'Thermoregulation in the Namib Desert golden mole Eremitalpa granti namibensis (Chrysochloridae)' and is co-authored with J.P. Waggoner, M.R. Perrin, and G.C.Hickman.

questioned this interpretation and suggested that low metabolic rate is an energy saving adaptation in response to limited resource availability and the high energy expenditure concomitant with burrowing. Finally, a low metabolic rate could represent an adaptation to the hypoxic and hypercapnic conditions typical of burrow atmospheres (Arielli, Arielli, Heth & Nevo, 1984; Baudinette, 1972).

Given such possible physiological determinants, the metabolic and thermoregulatory capacities of the Namib mole, *Eremitalpa granti namibensis*, are of particular interest. *E.g. namibensis* inhabits an arid sand dune environment and has diverged somewhat from the subterranean habitat typical of other African golden moles (Family Chrysochloridae). The Namib mole does not dwell in a sealed burrow system, but is nocturnally active on the dune surface searching for insect prey. Daylight hours are spent buried in loose shifting dune sand. In the present study, the bioenergetic characteristics of *E.g. namibensis* are examined to evaluate their significance as adaptations to a psammophilous habit in a thermally demanding but energy sparse environment.

MATERIALS & METHODS

Field Studies

Body temperature determinations

Adult *E.g. namibensis* were caught by hand in the Namib dunes at Gobabeb and Far East during 1983 and 1984. Time and date of capture, depth and temperature of sand from where the animal was excavated, and location of capture (in open sand or under a vegetation clump) were noted. Body temperature (Tb) of freshly caught individuals was obtained by inserting a sheathed type 'K' thermocouple 5mm into the cloaca. The thermocouple was attached to a Digitron 1408 thermometer accurate to $\pm 0.01^{\circ}C$. Each Tb measurement typically required 15 seconds handling time.

To examine the relationship between Tb and Ta one individual was placed into a 12ℓ bucket filled with dune sand. The open container was buried almost to its rim in a dune, and kept shaded during the day to prevent overheating from the $38-40^{\circ}C$ air and $50-60^{\circ}C$ surface sand temperatures. The animal was removed from the container every two hours and Tb recorded along with sand temperature in the bucket where the mole had been resting. Rectal and sand temperatures were monitored for 36 hours.

Microenvironmental measurements

At a site approximately 8km from Gobabeb, surface and subsurface (30, 20 and 10cms) sand temperatures were measured employing a data logger (Campbell CR-21) equipped with four thermistor probes accurate to $0.01^{\circ}C$. Thermistor probes were attached to a thermally inert rod buried vertically in the dune. The rod was located on level sand on an east facing upper dune slope approximately 2m distant from the nearest vegetation. An equilibration period of four hours preceded recording. Readings were taken every hour for 24 hours during a typical summer (January, 1984) and winter day (July, 1984).

A comparison of thermal conditions between non-vegetated and vegetated dune areas involved simultaneous measurements of sand temperatures at surface and 10 and 20cm depths beneath a clump of perennial dune grass (Stipagrostis sabulicola) having a basal area of $0.75m^2$ and in an area of unvegetated sand approximately 1m distant. Readings were taken over a 24 hour period (March 1987) using the procedure described above.

Laboratory Studies

Metabolic determinations

Heat production or standard metabolic rate (Bligh & Johnson, 1973) was measured by recording oxygen consumption rates (VO_2) of post absorptive moles (mean mass 24.6g, range 17-40g) over an ambient temperature (Ta) range of 10-40°C. Since E.g. namibensis is nocturnal, all measurements were made during daylight hours (08h00 - 12h00). The respirometer chamber was a large glass bell jar (volume 2100 cm^3), sealed with an O ring clamp system and equipped with an outlet port for extraction of air samples; a sachet of soda lime was enclosed for absorption of exhaled carbon dioxide. The chamber was placed in a dimly illuminated constant temperature cabinet controlled to ±1°C of the required Ta. After a three hour acclimation period at each Ta, (reduced to half an hour at stressful Ta's of greater than 30°C) animals were weighed and then sealed individually in the respirometer for approximately one hour. Prior to removing the mole from the test chamber, three 50ml gas samples were extracted through the outlet port with a syringe. Using a static sampling system, gas samples were injected into a Beckman OM-14 paramagnetic oxygen analyser. Before entering the oxygen analyser, each sample was dried by passing it through a column of anhydrous silica gel. The first 10ml of each sample cleared the 'dead space' around the silica crystals of air from the previous sample; the remaining 40ml was then injected into the oxygen analyser evenly over a 10 second period and any displacement from the 20.93% O_2 calibration value used to calculate oxygen consumption. Oxygen consumption rates were expressed as $cm^3O_2g^{-1}hr^{-1}$ after correction to S.T.P. Although the apparatus used did not allow for measurement of VO_2 in conjunction with associated activity patterns, most animals remained inactive during experimental runs. Data from individuals that showed any sign of activity or agitation were discarded. Therefore values of standard metabolic rates are if anything slightly overestimated. Body temperature of test animals was recorded after each VO_2 measurement. The temperature in the respirometer, although not monitored continuously during experimentation, was recorded immediately upon removal of the animal from the chamber.

In a second series of experiments, VO_2 rates of animals submerged in sand were measured. Experimental protocol was similar to that described above, excepting that animals were provided with

166cm^3 of Namib dune sand during both the periods of acclimation and VO_2 measurement. Prior to extraction of gas samples, the bell jar was gently shaken for a few seconds to ensure complete mixing of air.

Thermal preferenda

The temperature gradient chamber for determination of thermal preferenda of E.g. namibensis consisted of a circular run (10cm width, 95cm outer diameter) partitioned into two halves which enabled monitoring of two animals simultaneously (Fig. 5.1). The floor of each half run contained 16 copper tubes arranged in parallel fashion and covered to a depth of 4cm with dune sand. A circular temperature gradient was maintained in each semicircular chamber by controlling the rates of hot and cold water pumped through the counter current tubing (hot water was supplied by a lauda circulating water bath, Model NB4; a 40ℓ bucket of ice water provided the cold water). Sand temperatures at the cool and warm ends of the chamber were maintained at 20°C (±1°C) and 38°C (±1°C) respectively. Animals were placed in the temperature gradient for at least one hour prior to any body temperature determinations. After acclimation, body temperatures of the moles were measured hourly for 24 hours (during which food was not provided) and the position of the mole in the gradient recorded.

Diurnal variation in body temperature

Diurnal Tb variation was measured in E.g. namibensis housed in

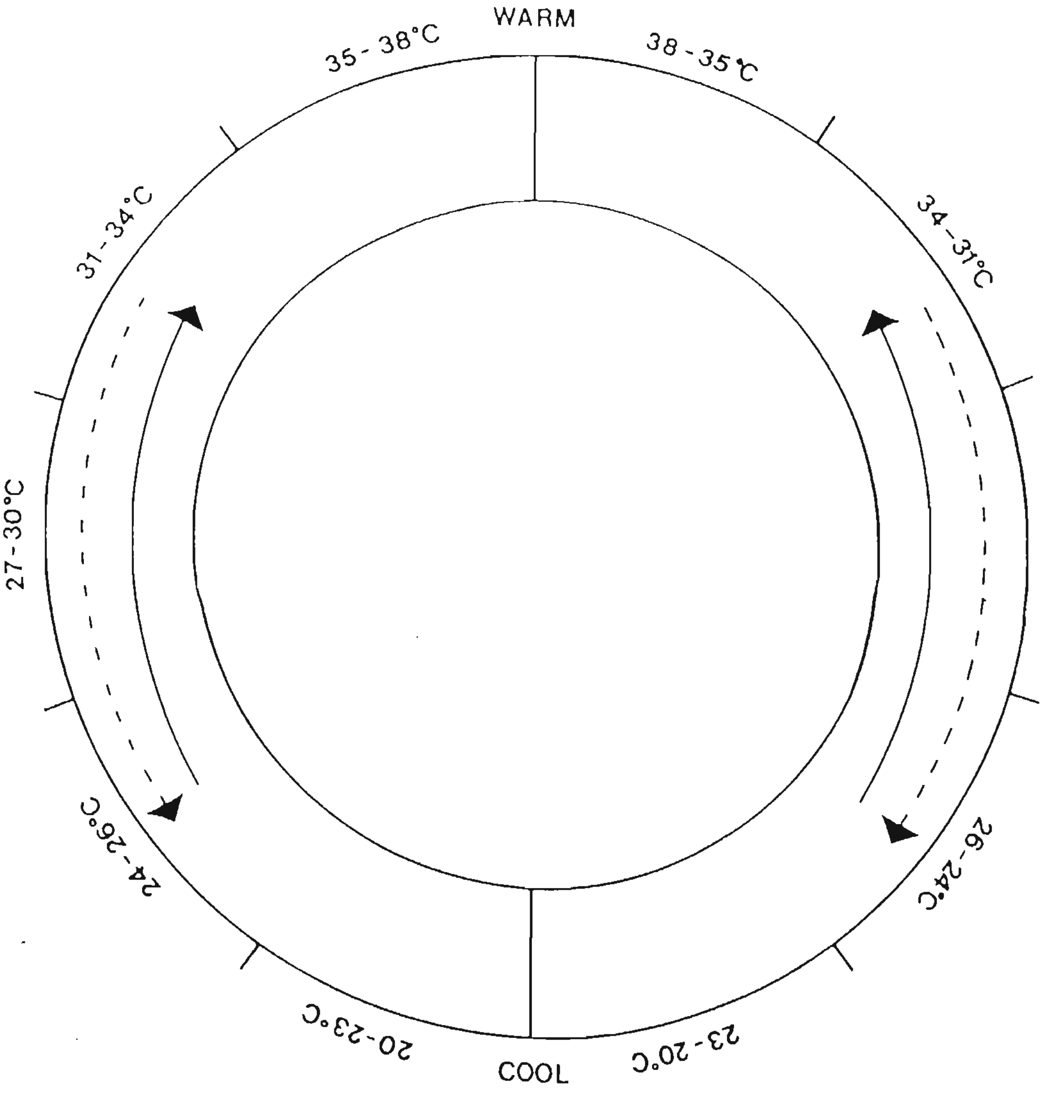

FIGURE 5.1: Diagrammatic representation of temperature gradient chamber partitioned into two halves with approximate range of temperatures indicated. Arrows show direction of hot (broken line) and cold (solid line) water flow in copper tubing.

a windowless constant temperature room at Ta 21^{o}C, ambient humidity, 30-50% R.H., and a 12 hour photoperiod with light from 07h00 - 19h00. Animals were kept individually in 9 plastic buckets filled nearly to capacity with Namib sand; mealworms (*Tenebrio molitor* larvae) were provided daily at 17h00 and any excess removed at the next feeding time. The Tb of each animal was measured on 12 occasions over a period of two weeks; the times of measurement were distributed uniformly throughout the day-night cycle.

RESULTS

Field Observations

Body temperatures of animals just after capture were variable and ranged from 19.2^{o}C to 38.2^{o}C (Fig. 5.2). These measurements were generally representative of animals caught between 08h00 and 10h00 since later in the day, dune surface glare and afternoon winds made it difficult to locate areas where moles were buried. Summer individuals (November - April) had a mean Tb of 29.7^{o}C (S.D.$\pm$4.5) which was significantly different (Student's t-test: $t=3.98$; $p<0.001$; d.f.=21.00) from a mean Tb of 22.1^{o}C (S.D.$\pm$3.5) for winter individuals. A strong positive linear correlation was found between Tb and ambient sand (Ta) at depths where moles were located (Fig. 5.3). In 23 paired comparisons, no significant difference was observed between the two parameters (paired t-test: $t=1.47$; $p>0.05$; d.f.=22.00).

A frequency distribution of depths at which moles were captured (Fig. 5.4) indicated few animals at depths less than

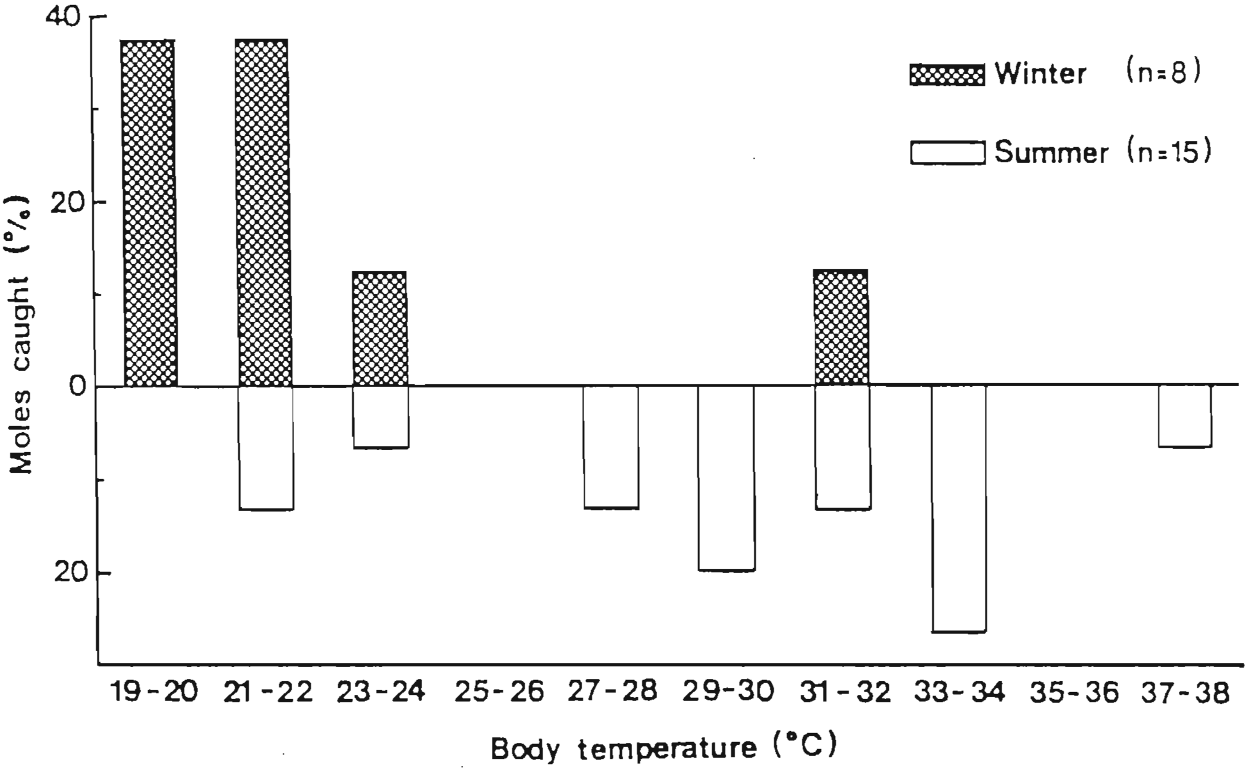

FIGURE 5.2: Body temperatures of _E.g._ _namibensis_ recorded immediately after capture for summer (November - April) and winter (May - October).

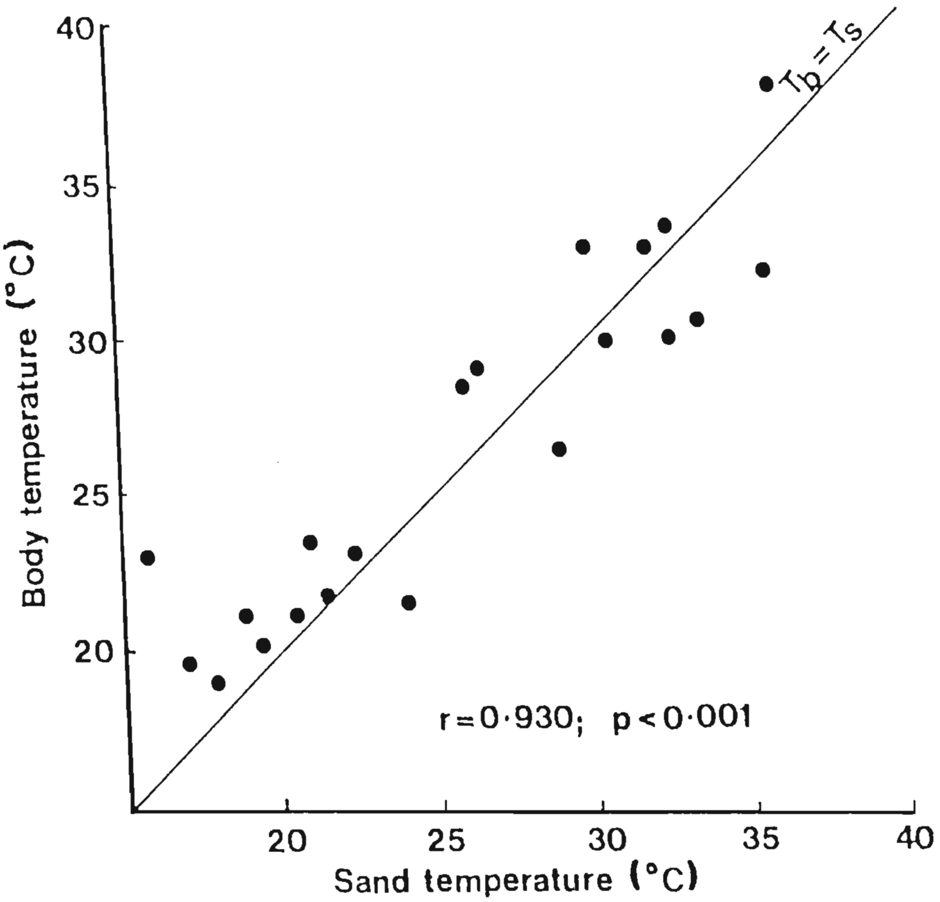

FIGURE 5.3: Relationship between sand and body temperature of freshly caught E.g. namibensis.

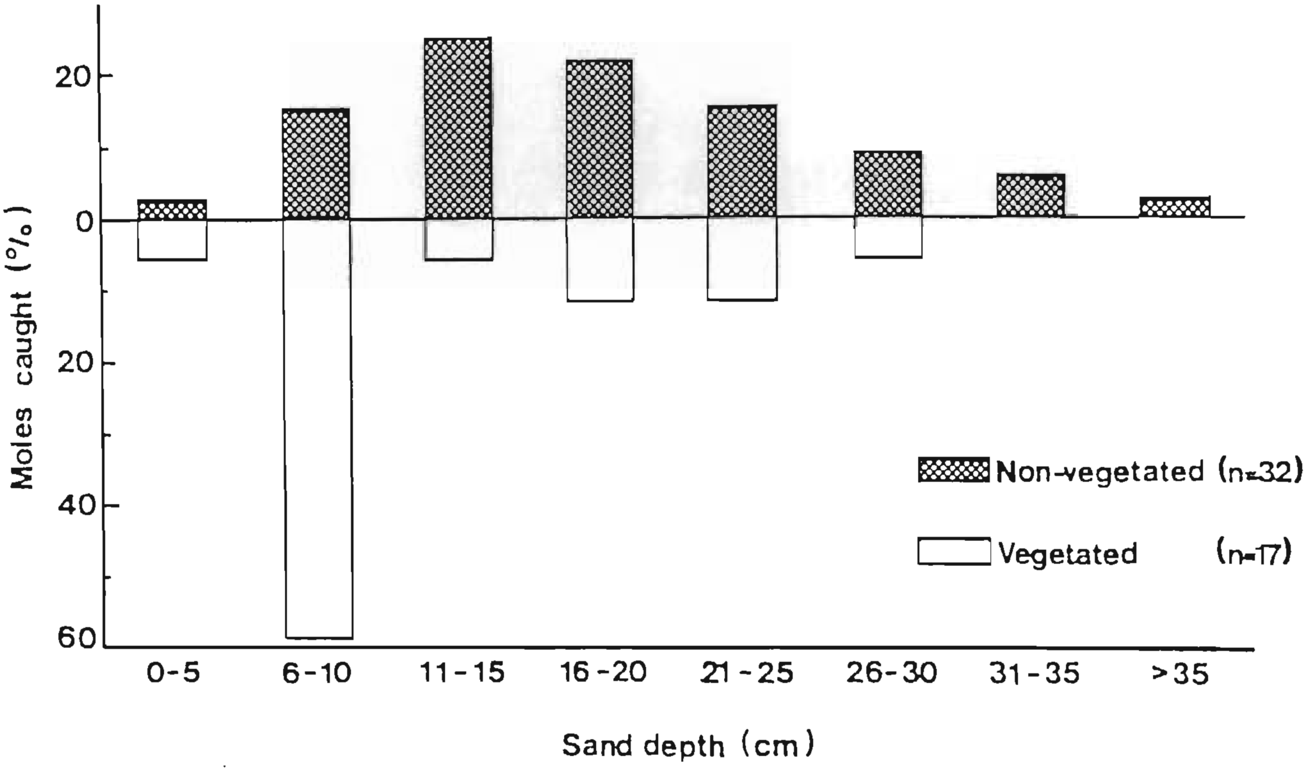

FIGURE 5.4: Subsurface depths at which E.g. namibensis were caught in the dunes both in vegetated and non-vegetated areas.

5cm or greater than 30cm (maximum 37cm and minimum 5cm). Moles excavated from beneath clumps of vegetation were at significantly (Student's t-test: $t=2.61$; $p<0.05$; d.f.=47) shallower levels ($\bar{x}=13.06$cm; S.D.± 7.04) than those in unshaded sand ($\bar{x}=19.21$cm; S.D.± 8.25).

Body temperatures of the specimen kept in a container of sand exposed to a natural thermally fluctuating environment ranged from 18.1°C to 31.6°C (Fig. 5.5). Body temperatures closely paralleled changes in sand temperatures and were on average 0.7°C (S.D.± 1.6) higher than sand. Differences between Tb and Ta were not statistically significant (paired t-test: $t=1.93$; $p>0.05$; d.f.=19). During the period of measurement, the mole rested near to the bottom of the bucket at about 20cm depth.

Microenvironmental Conditions

Winter and summer dune temperature profiles are given in Fig. 5.6. Summer surface diel temperature range was 40°C with measurements exceeding 50°C by midday. With increasing depth, thermal conditions were more moderate and stable. Mean summer temperature at 30cm was 34°C with a daily fluctuation of 1°C. Daytime surface temperatures were always higher than subsurface with the situation being reversed at night. In winter, maximum surface temperature was 16°C lower than in summer. Subsurface readings were approximately 8-10°C below summer measurements at corresponding depths.

Cooler thermal conditions beneath a clump of _S. sabulicola_ compared to those in nearby unshaded sand (Fig. 5.7)

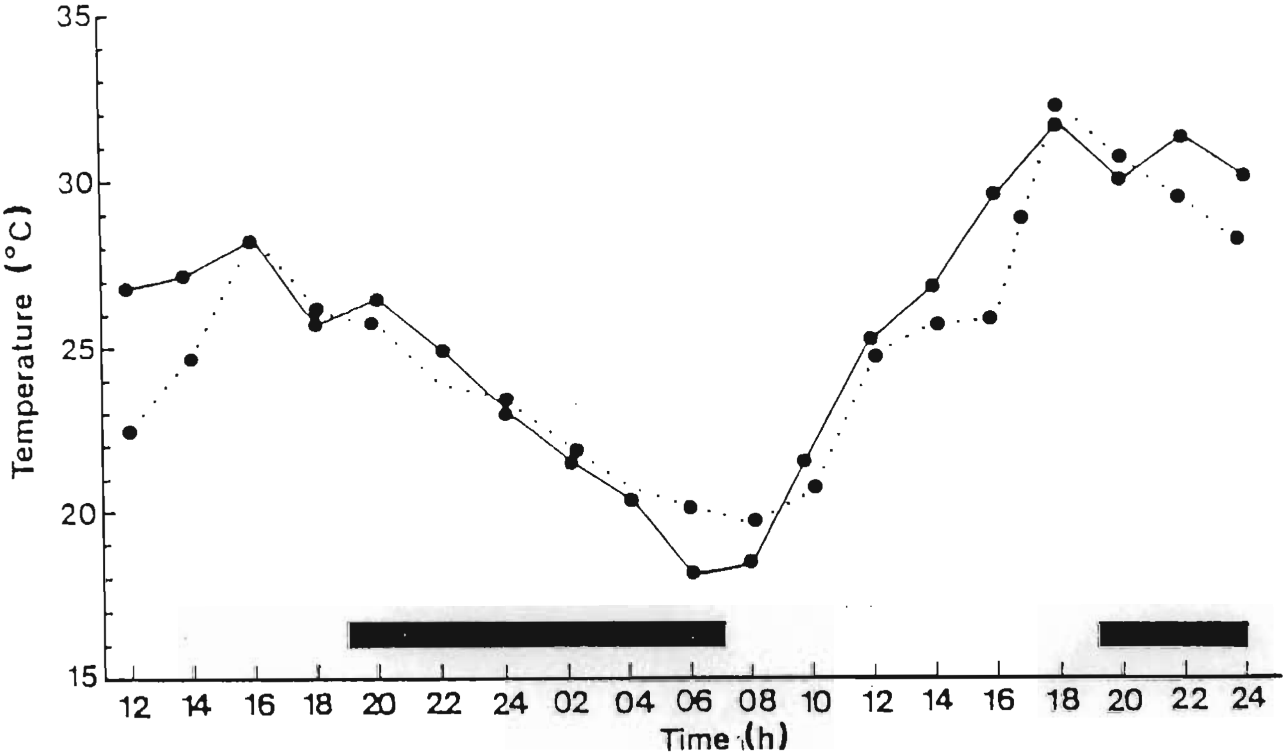

FIGURE 5.5: Daily variation of body (solid line) and sand (broken line) temperature of a single E.g. namibensis held captive in a plastic container submerged in a Namib dune (12-13 September 1984). Solid bars indicate nighttime.

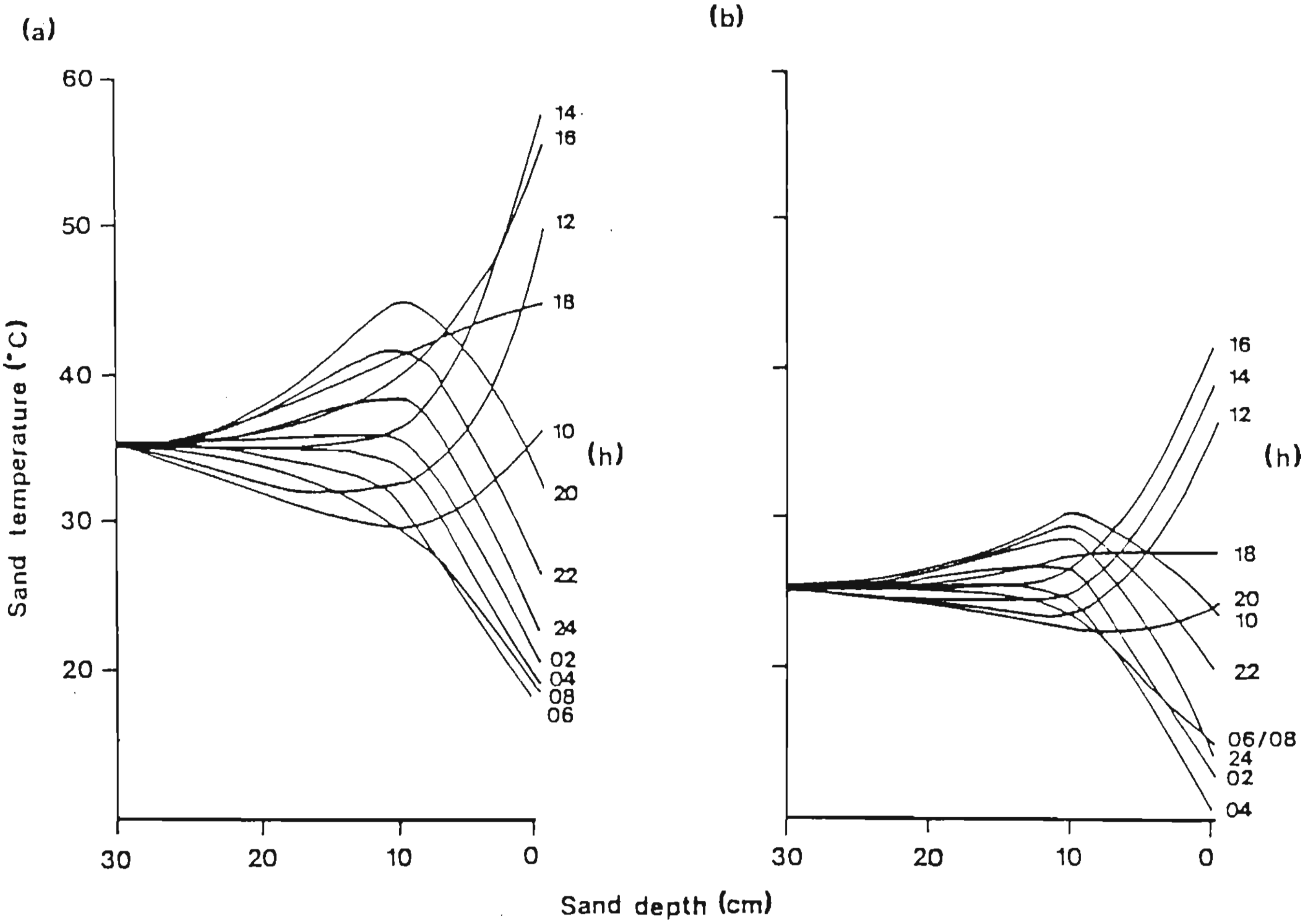

FIGURE 5.6: Temperatures of subsurface sand (0-30cm) on a dune slope in the Namib Desert during (a) summer (21-22 January 1984) and (b) winter (6-7 July 1984).

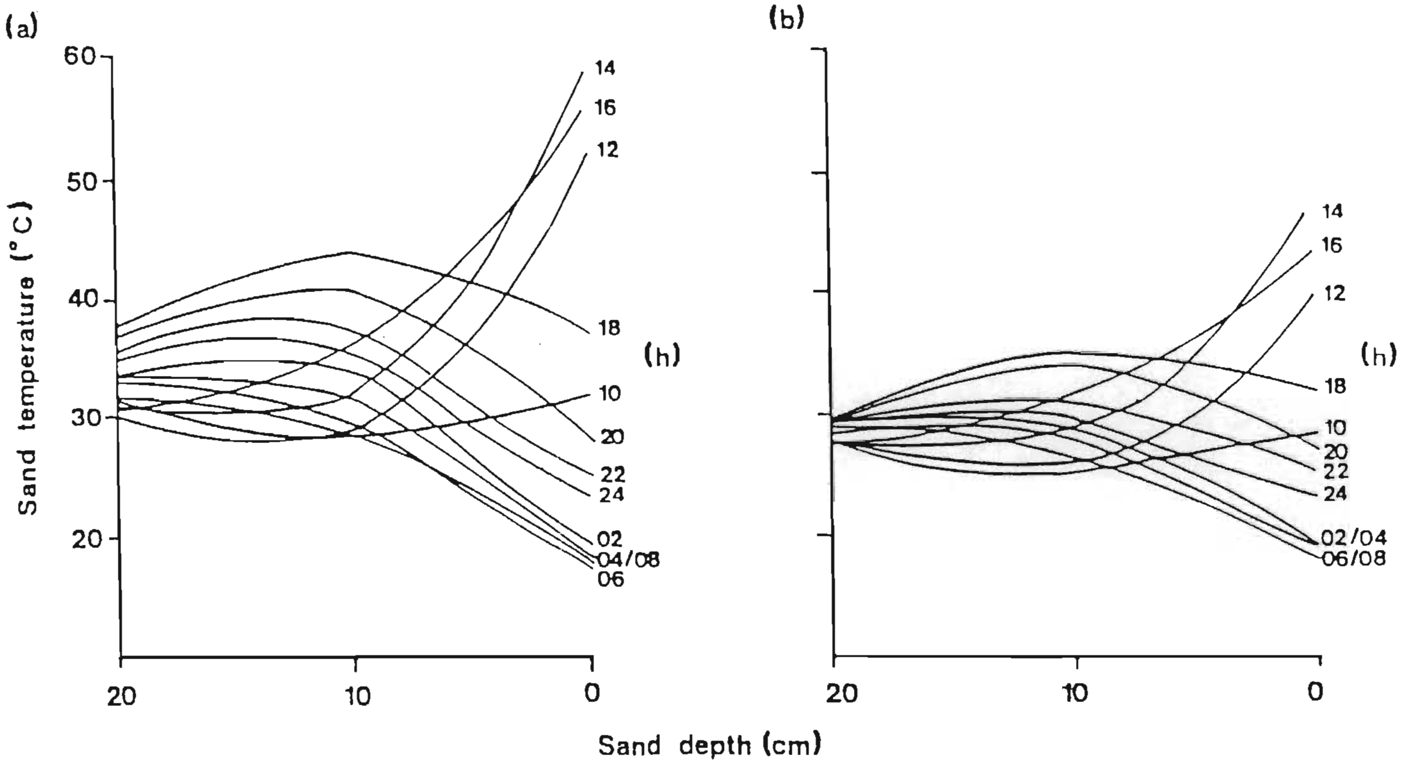

FIGURE 5.7: Temperatures of subsurface sand (0-20cm) in open sand (a) and beneath a clump of S. sabulicola (b) on a dune slope in the Namib Desert during summer (19-20 March 1987).

illustrate clearly the buffering effect of vegetative cover; maximum surface temperatures were 11°C lower with plant cover, while at 10cm depth the average temperature (29.4°C) was 4.7°C less than unshaded sand (34.1°C). Mean shaded and unshaded temperatures at 20cm depths were 29.1°C and 33.9°C respectively.

Metabolic Determinations

For moles out of sand, a basal metabolic rate of $0.52 cm^3 O_2 g^{-1} hr^{-1}$ (S.D.±0.09) was measured at Ta=31°C (Fig. 5.8). Below the thermoneutral point at 31°C the increase in VO_2 with reduced air temperature was non-linear with the rate of change in VO_2 being less at Ta=15°C than at Ta=22°C and 26°C. Below 15°C, heat production declined rapidly and showed no increase relative to that at Ta=31°C.

For moles in sand, a thermoneutral zone rather than point was evident. Thermoneutrality was estimated to lie between Ta 31 -36°C, since no statistical difference was observed between VO_2 at these temperatures (Student's t-test: $t=0.46$; $p>0.05$; d.f.=11). The average resting metabolic rate in thermoneutrality was 0.59 (S.D.±0.21) $cm^3 O_2 g^{-1} hr^{-1}$ which was not significantly different from the basal out of sand metabolism (Student's t-test: $t=0.69$; $p>0.05$; d.f.=17). Below thermoneutrality, changes in VO_2 followed a similar pattern to that recorded out of sand excepting that rates of metabolism were significantly lower than those out of sand at Ta's below 25°C (Student's t-test: $p<0.01$ at 22°C; $p<0.001$ at 15°C; $p<0.05$ at 9°C), and moles were unable to sustair

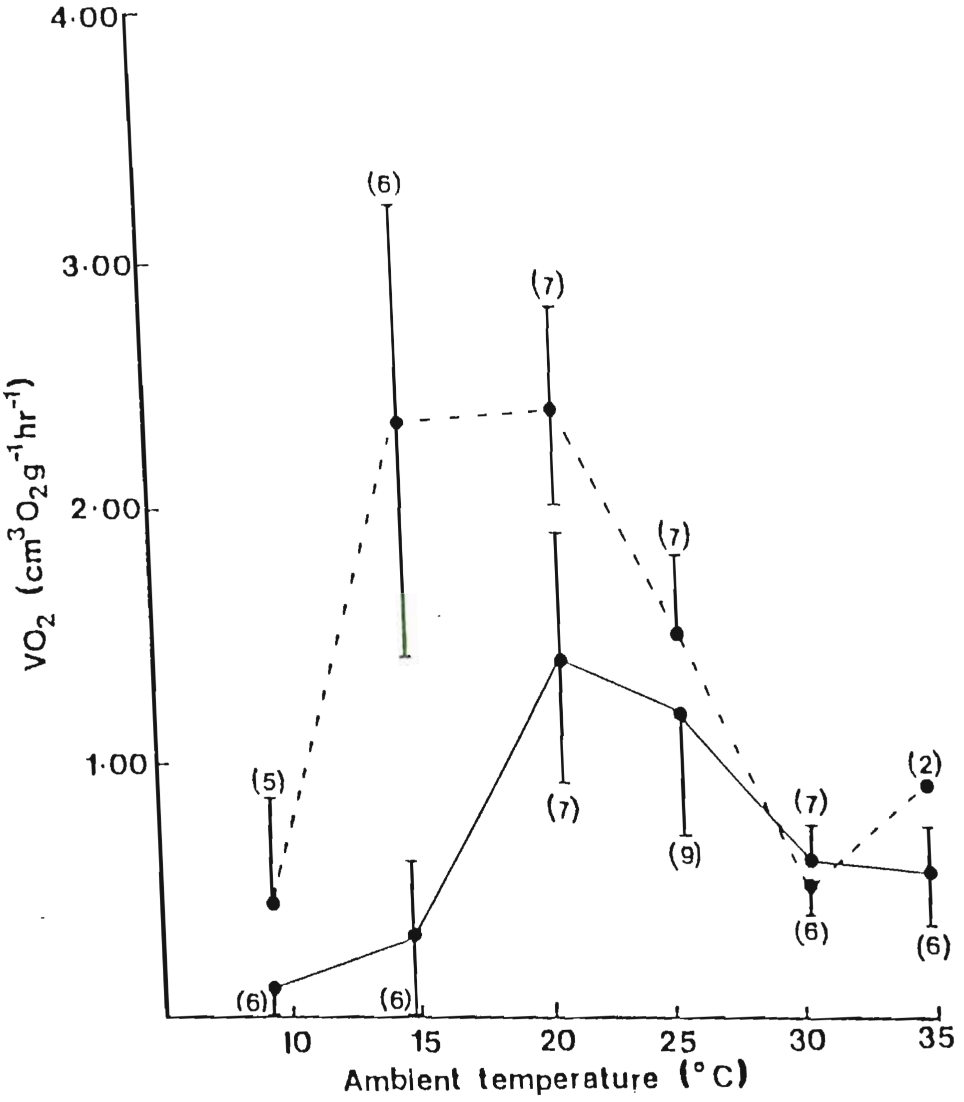

FIGURE 5.8: Oxygen consumption of E.g. namibensis in (solid line) and out (broken line) of sand at different ambient temperatures. Results expressed as the mean ± 1 S.D.. Numbers in parentheses indicate sample size.

elevated VO_2's at Ta's below 20°C.

Body temperatures were extremely labile (range 10.9-37.7°C) and varied directly with Ta (Fig. 5.9). The slope of the regression of Tb on Ta for moles in sand differed significantly from that out of sand (Student's t-test: $t=2.12$; $p<0.05$; d.f.=70) showing that the rate of decline in Tb with decreasing Ta was greater for moles in sand. Body temperatures out of sand were significantly higher than those in sand over the Ta range 31-15°C (Student's t-test: $p<0.01$ at 31 and 15°C: $p<0.02$ at 26°C: $p<0.001$ at 22°C). Fatalities from heat exposure occurred at 36°C out of sand but only at 40°C in sand. At these stressful temperatures, the bare feet and nose became bright pink due to peripheral vasodilation, while the throat and chest regions became wet as a result of salivation. Unfortunately Tb and VO_2 measurements were not obtained for animals which died of heat stress since death was not noted until removal from the respirometer chamber.

Based on field and laboratory observations, a temperature ethogram for E.g. namibensis is given in Table 5.1. At Tb's as low as 26°C, moles were fully alert and capable of normal co-ordinated movement. Below 26°C, alertness and co-ordination began to decline until at Tb's below 15°C, moles were completely unresponsive and made no attempt to dig when placed in sand. Metabolic and behavioural responses at Tb's below 10°C were not investigated.

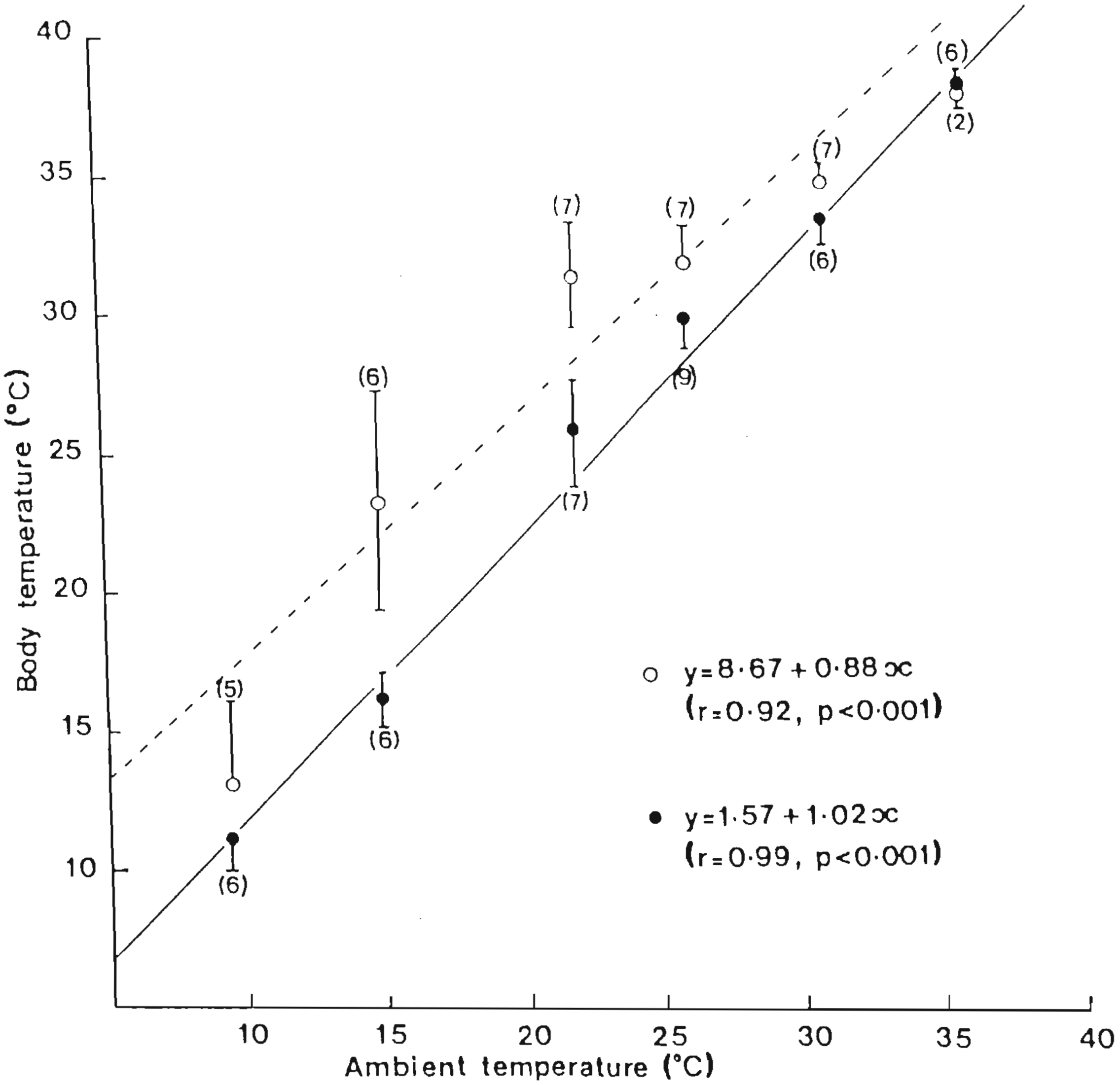

FIGURE 5.9: The relation of body to ambient temperature in E.g. namibensis during measurements of oxygen consumption. Results expressed as the mean ± 1 S.D. (solid circles in sand, open circles out of sand). Numbers in parentheses indicate sample size.

TABLE 5.1: Temperature ethogram for E.g. namibensis based on field and laboratory observations

Tb (^{o}C)	Characteristics, behaviour
10 - 14	Stiff, motionless, completely unresponsive, breathing undetectable.
15 - 19	Slow and very sluggish movements. Will attempt to dig into sand, capable of vocalisation. Weak shivering.
20 - 25	Moves slowly, movements slightly unco-ordinated. Able to dig into sand. Shivers strongly when resting.
26 - 29	'Normal' movements. Shivers strongly when resting.
30 - 38	Extremely active. No shivering.
39 +	Fatality

Thermal Conductance

Physical laws of heat exchange (i.e. Newton's law of cooling) state that the temperature of a body at equilibrium is determined by the rate of heat exchange, the difference between body and ambient temperature, and the thermal conductance, i.e. for an animal, HP= C(Tb-Ta) where HP is the rate of heat production and C is thermal conductance. The value C is most accurately calculated as $VO_2/(Tb-Ta)$ (McNab, 1980a) and such values for E.g. namibensis over the various experimental conditions are summarised in Table 5.2 (measurements included heat loss through evaporation and thus are 'wet conductances'). Both in and out of sand, C varied widely at different Ta's due to variable Tb. McNab (1980a) has pointed out that in endotherms that regulate body temperature poorly, decrease in C with decrease in Tb and VO_2 is presumably due to a reduced heart rate, rather than as a result of an active reduction in conductance per se. Thus, when examining differences in C between animals in and out of sand, it seemed inappropriate to make comparisons at Ta's with significant discrepancies between VO_2 measurements. For these reasons, comparisons of C were restricted to Ta's of 26-31°C. Under such conditions, conductances in sand were found to be significantly higher (Student's t-test: $t=3.37$; $p<0.01$; d.f.=27).

Thermal Preferenda

During temperature selection experiments, moles spent most of the time buried in the sand sleeping. Approximately 20% of

TABLE 5.2: Comparison of thermal conductance (C) for *E.g. namibensis* in and out of sand at different ambient temperatures. Values expressed as the mean ±1 S.D.(n)

Ta (^oC)	C ($cm^3O_2g^{-1}hr^{-1o}C^{-1}$) In sand		Out of sand	
9	0.04±0.02	(6)	0.08±0.05	(5)
15	0.33±0.39	(6)	0.27±0.07	(6)
22	0.38±0.11	(7)	0.27±0.08	(7)
26	0.45±0.20	(9)	0.30±0.09	(7)
31	0.42±0.16	(7)	0.17±0.06	(6)
36	0.52±0.19	(6)	0.44±0.01	(2)

the time was spent sandswimming or running vigorously on the surface. Four of five animals tested usually selected sand temperatures between 31-38°C for resting (Fig. 5.10). A fifth individual showed a preference for the cooler parts of the thermal gradient and exhibited Tb's of 30.5-19.3°C (Fig. 5.11) with a mean Tb of 22.1°C (S.D.±2.5°C). In contrast, moles favouring warm conditions maintained high and relatively stable Tb's. No significant difference was observed between measurements for these four individuals (one-way anova: $F=1.62$; $p>0.05$; d.f.=3,92) with mean Tb's between 30.8-33.3°C and averaging 32.4°C (S.D.±1.2°C). This value of 32.4°C corresponded closely to the Tb of 33.2°C measured in the lower zone of thermoneutrality for moles submerged in sand (Fig. 5.9) and is considered to be the 'preferred' temperature.

Diurnal Variation in Body Temperature

Diurnal changes in Tb at constant low Ta are shown in Fig. 5.12. Although there was considerable variation in Tb between the four individuals at every sampling time, a clearly marked daily rhythm in Tb was evident. During the period of darkness, Tb's were considerably lower and less variable than during daylight hours, and generally remained within 1 or 2°C of ambient temperature. Body temperatures were highest between midday and early evening.

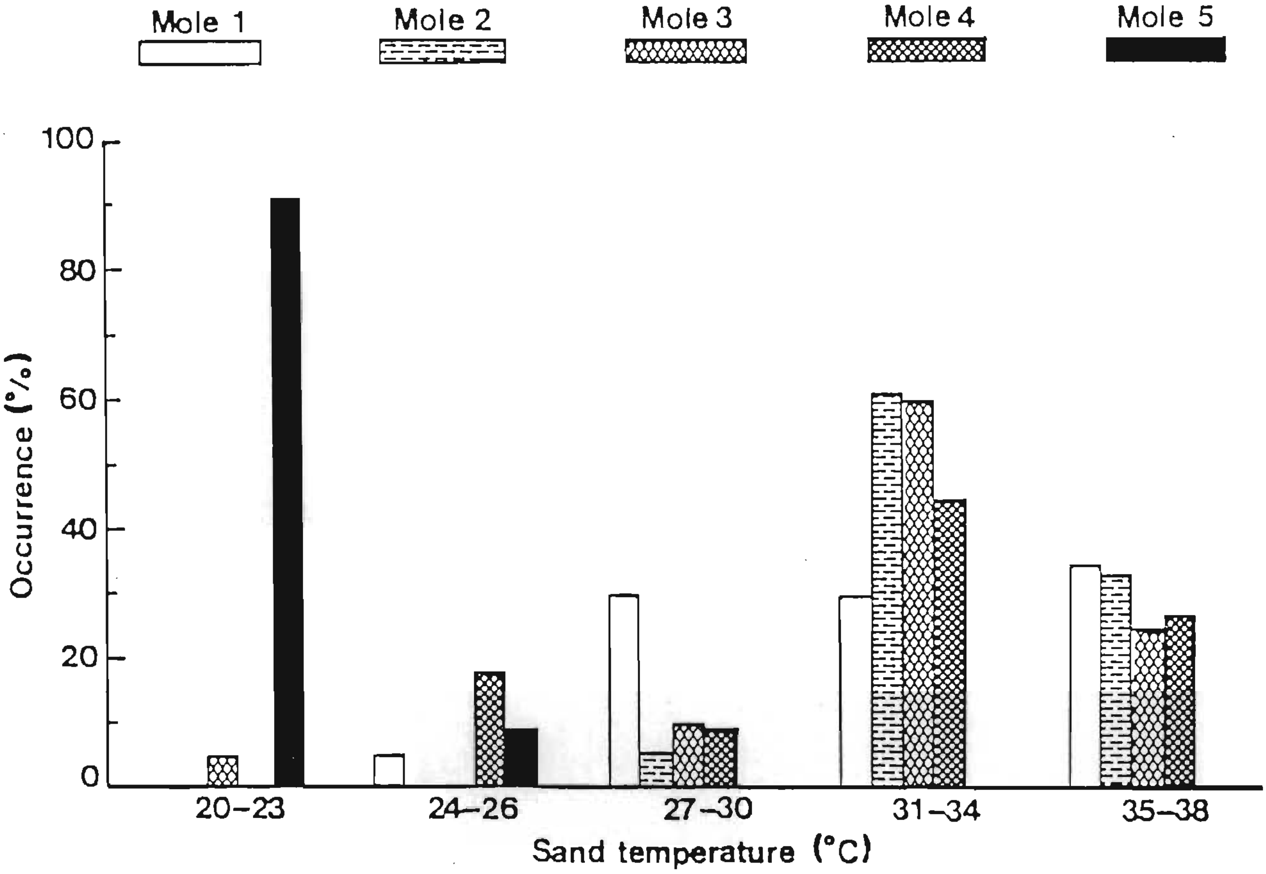

FIGURE 5.10: Temperature selection in resting E.g. namibensis placed in a thermal gradient for 24 hours. Relative frequencies of location of moles in gradient calculated from observations at one hour intervals.

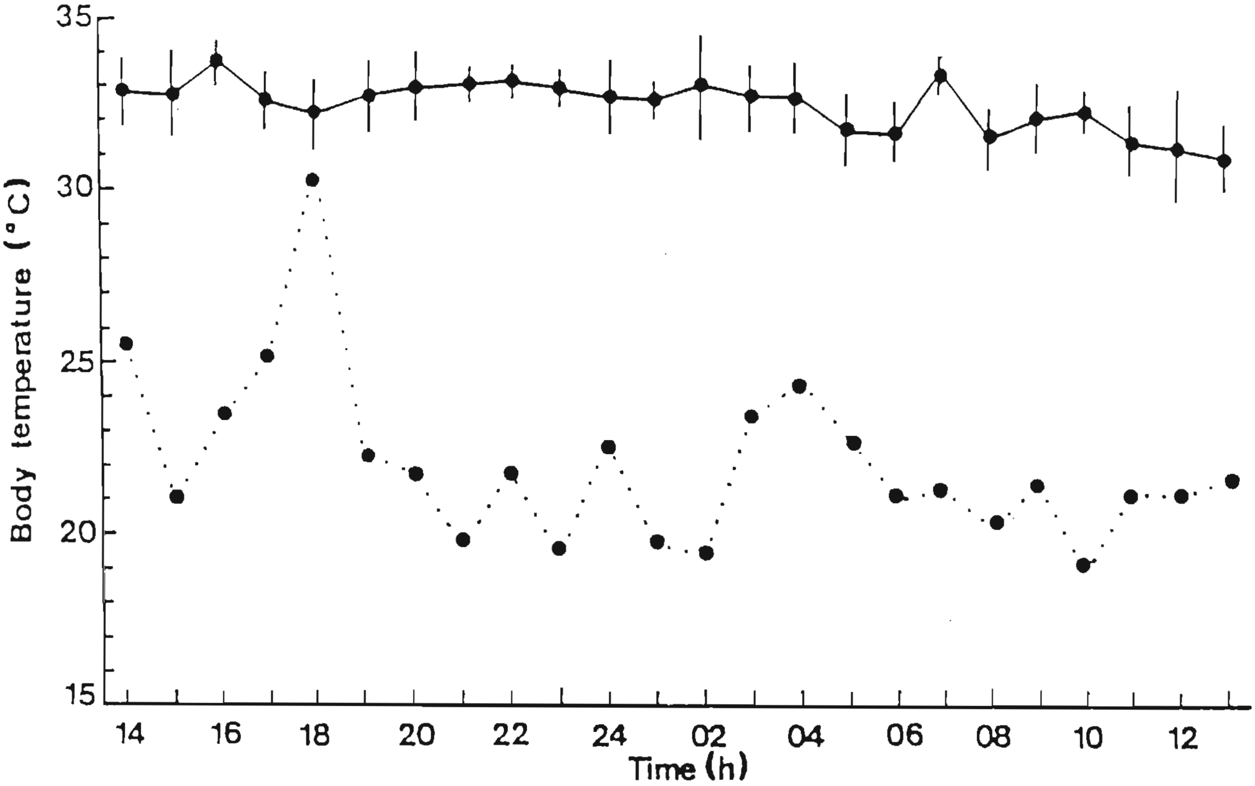

FIGURE 5.11: Body temperature of E.g. namibensis during 24 hours in a 20-38°C thermal gradient. Means ± 1 S.D. given for moles 1-4 (solid line), mole 5 (broken line).

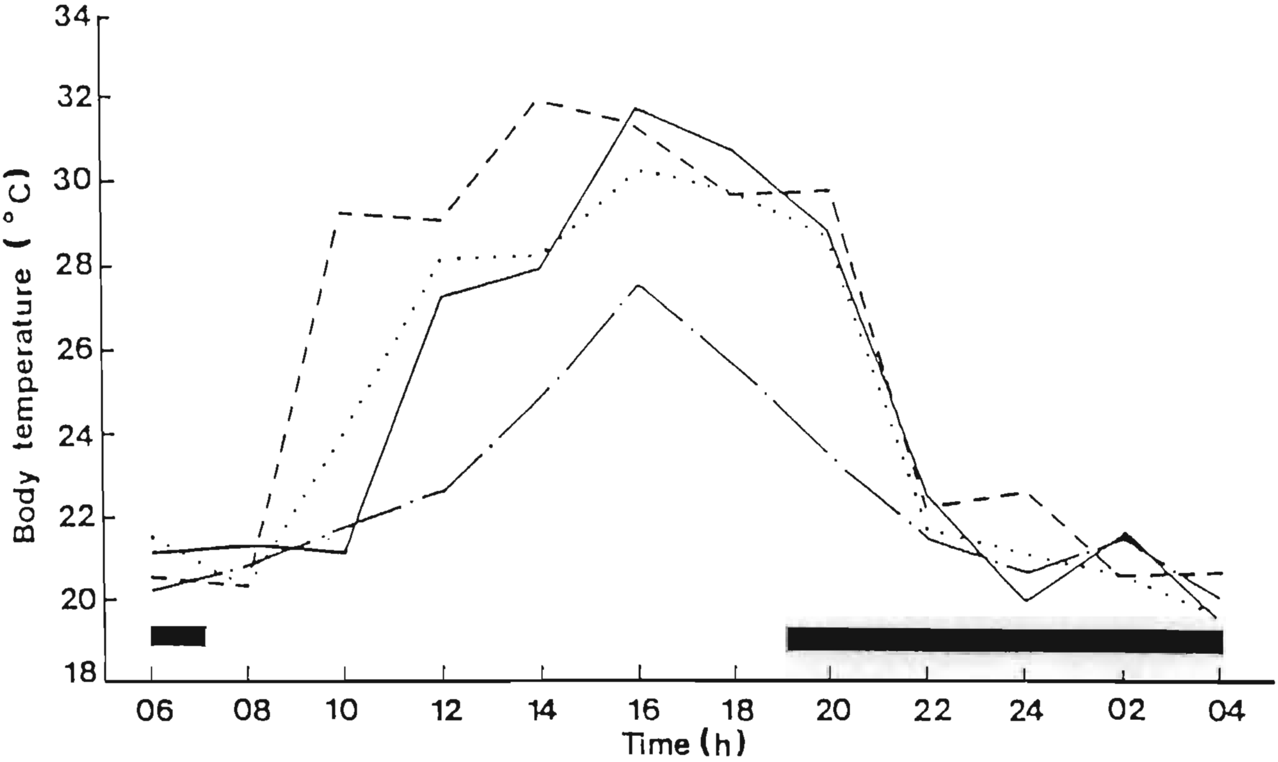

FIGURE 5.12: Variation in body temperatures of four E.g. namibensis in a constant sand temperature of ±21°C. Sampling times are given along bottom axis. Solid bar indicates period of darkness.

DISCUSSION

Primitive or Specialised?

The lability of VO_2 and Tb in E.g. namibensis has previously been shown for the mesic dwelling, but closely related, Cape golden mole (Chrysochloris asiatica) (Withers, 1978) and the Hottentot golden mole (Amblysomus hottentotus) (Kuyper, 1979, 1985). Although body temperatures of these two species are somewhat dependent on Ta, they usually choose to maintain a Tb greater than 30°C at ambient temperatures as low as 5°C. Data from this study indicate that ambient temperatures below 15°C are completely beyond the regulatory capacity of E.g. namibensis.

Withers (1978) maintained that the poor thermoregulatory abilities of golden moles, like that of another family of insectivores, the Tenrecidae (Eisenberg & Gould, 1970; Hildwein, 1970; Jagger, Taylor & Crompton, 1974) is attributable to their evolutionary status as 'primitive mammals' with low metabolic rates representing an intermediate stage between other eutherian mammals (high energy turnover) and reptiles (low energy turnover). However, McNab (1978, 1980b) argued convincingly that poor temperature regulation of certain mammalian groups is in fact adaptive and related to environmental factors as opposed to being a phylogenetic legacy. Indeed, many taxa of mammals considered primitive are capable of well maintained and precise homeothermy, for example monotremes (Grant & Dawson, 1978a), elephant shrews (Leon, Shkolnik & Shkolnik, 1983), hedgehogs (Shkolnik, 1980) and marsupials (Hulbert & Dawson, 1974a). Conversely certain advanced and highly specialised taxa such as the naked mole rat (*Heterocephalus glaber*), exhibit poor thermoregulatory capabilites (Withers & Jarvis, 1980).

An examination of the metabolic characteristics of the three chrysochlorid species studied to date (Table 5.3) favours the arguments of McNab (1978). The higher than expected thermal conductances, together with low Tb's (and in the case of *E.g. namibensis* and *C. asiatica* lower than expected BMR's) are physiological traits characteristic of many other subterranean taxa (Bradley, Miller & Yousef, 1974; Haim & Fairall, 1986; McNab, 1966, 1979; Nevo, 1979) and are believed to have evolved as a result of similar selection pressures concomitant with the subterranean milieu.

The very low basal metabolic rate of *E.g. namibensis* greatly exaggerates the trend found in most subterranean mammals, but seems consistent with the findings of Lovegrove (1986), that aridity related factors are instrumental in selecting for low metabolic rates in desert species. Specifically which physical or ecological determinant of the Namib dune environment is favouring the unusual physiological traits of *E.g. namibensis* requires an evaluation of existing hypotheses concerning the energetics of subterranean mammals.

Thermal Stress Hypothesis

Burrows of subterranean mammals are usually near saturation with water vapour (Dubost, 1968; Kennerly, 1964). Under such

TABLE 5.3: Basal metabolic rates (BMR: $cm^3 O_2 g^{-1} hr^{-1}$), thermal conductances (C: $cm^3 O_2 g^{-1} hr^{-1} {}^oC^{-1}$) and body temperatures (Tb: ^oC) of three species of golden mole

Species	mass(g)	BMR	% expected[b]	C[c]	% expected[d]	Tb[e]	Reference
Eremitalpa granti namibensis[a]	26.1	0.52	22	0.30	158	34.7	This study
Amblysomus hottentotus	69.8	1.37	103	0.15	120	33.5	Kuyper 1979, 1985
Chlorotalpa asiatica	36.0	1.20	62	0.25	151	35.0	Withers 1978

[a] Values given for animals out of sand

[b] Expected BMR calculated from $BMR=15.67W^{-0.582}$ based on values for 26 species of insectivores (Hayssen & Lacy, 1985).

[c] Minimum wet conductance estimated below thermoneutrality at Ta 25°C for *E.g. namibensis* and *C. asiatica* and 20°C for *A. hottentotus*.

[d] Expected C calculated from $C=0.760W^{-0.426}$ based on values for 180 mammalian species (Bradley & Deavers, 1980)

[e] Body temperature at lower limit of thermoneutrality.

circumstances, evaporative cooling is unlikely to be of much importance. Indeed many species of subterranean rodents place little reliance on evaporative water loss as a means of dissipating endogenous heat production and usually become hyperthermic at ambient temperatures above thermoneutrality (Contreras, 1986; Gettinger, 1975). McNab (1979) proposed that low metabolic rate, high thermal conductance and low body temperature are important mechanisms to prevent overheating in warm humid burrow systems where the potential for evaporative and convective cooling is reduced. Thus in very warm environments, such as that occupied by _H. glaber_ (McNab, 1965), prevention of thermal stress requires such a radical combination of small size, high thermal conductance and low metabolism, that poor thermoregulatory abilites and labile body temperature result.

Relative humidities of between 46-25% have been reported at depths of 10cm in Namib sand dunes (Robinson & Seely, 1980; Seely & Mitchell, 1987), but these values are representative of conditions in relatively dry, highly mobile sand on a dune slipface. Within the confined microenvironment of a mole resting submerged in sand, accumulation of respiratory water vapour may result in near saturation levels. In such a situation, evaporative heat loss may be of little importance. Indeed, heat dissipation by evaporative water loss does not appear to be very effective in _E.g. namibensis_, since even salivating was insufficient to prevent hyperthermia at temperatures above thermoneutrality. Cooling was further hindered by the absence of sparsely haired extremities other than the small naked feet and nose. Out of sand, *E.g. namibensis* was not able to tolerate ambient temperatures greater than 36°C which is below the 38-40°C typical for small mammals (Hudson & Rummel, 1966; Lee, 1963; McNab & Morrison, 1963), but similar to the 34-36°C range reported for *C. asiatica* (Withers, 1978), *A. hottentotus* (Kuyper, 1979) and other species of subterranean mammals (McNab, 1966).

Thermal conductance, as a measure of the ease of heat transfer from an animal, seldom reflects a constant physiological property but is also dependent on environmental variables as well (Tracy, 1971). For instance, Grant and Dawson (1978b) demonstrated a two to fivefold increase in thermal conductance in water as compared to air in the platypus (*Ornithorhynchus anatinus*). Similarly, when submerged in sand, the physical properties of this substrate (high conductivity and high specific heat; Stolzy & Jury, 1982) enhance heat transfer in *E.g. namibensis*. Since higher values of thermal conductance were not compensated by higher rates of heat production, moles in sand exhibited lower body temperatures than moles out of sand at similar ambient temperatures. The resulting smaller temperature differential (Tb-Ta) effectively extended the thermal tolerance of *E.g. namibensis* to environmental temperatures of between 39-40°C.

Summer temperatures in the superficial sand layers rise above 40°C, but moles can easily avoid these extremes by burrowing to deeper levels. Mean depths at which moles were excavated in unshaded sand (±19cm) corresponded to summer temperatures averaging 34-35°C measured in the present study to the somewhat lower 32°C reported by Robinson and Seely (1980). These temperatures lie well within the zone of thermoneutrality measured for E.g. namibensis in sand, and do not differ markedly from summer burrow temperatures (32°C) of A. hottentotus in Natal (Kuyper, 1979). Favourable thermal conditions exist at even shallower depths (±13cm) underneath plants. Apart from predator avoidance moles may favour refuge under vegetative cover (Chap. 3) to minimise required depth for avoidance of stressful temperatures. Furthermore nocturnality allows avoidance of high temperatures when emerged on the sand surface.

For the above reasons, it is suggested that avoidance of thermal stress is not the main factor favouring lowered metabolic rates and high thermal conductance in E.g. namibensis, since it is unlikely that moles are exposed to unfavourable temperatures under natural circumstances. Furthermore, tolerance of E.g. namibensis to high temperatures is a consequence of the physical properties of sand. Out of sand, Namib moles show no better ability to cope with stressful temperatures than do other chrysochlorid species.

Adaptations to Hypoxia and Hypercapnia

The primary means of gas exchange in the plugged burrow systems of subterranean mammals is by diffusion through soil

(Boggs, Kilgore & Birchard, 1984). Often diffusion is not sufficient to prevent large gradients of respiratory gas build-up, resulting in high CO_2 and low O_2 concentrations (Arielli, 1979; Schaefer & Sadlier, 1979). Low metabolic rates in subterranean mammals may serve to reduce total oxygen demand during hypoxia and decrease dependency upon high diffusion rates through soil (Baudinette, 1972; McNab, 1966; Nevo, 1979). Thermolability can also enhance physiological adaptations to hypercapnia since the ventilatory response to CO_2 in homeotherms is also greatly reduced in hypothermia (Lechner, 1976).

Compared to other soils, dune sand has a large percentage of its total pore space composed of macropores (usually filled with gases) as opposed to micropores (which generally contain water). This permits a faster exchange of water and gases, hence better aeration (Foth & Turk, 1972; Robinson & Seely, 1978). Indeed in the upper 20cm of the dune sand (where moles are usually found), air is continually being changed because the warmth of daytime drives some of the expanding and water laden air out of the dune, while fresh dry air is drawn in during nightly cooling (Bagnold, 1954). Thus it is unlikely that _E.g._ _namibensis_ is subject to conditions of hypoxia and hypercapnia any more severe than those found in subterranean burrow systems. In support of this conclusion, Arielli _et_ _al_. (1984) found that conditions of hypoxia and hypercapnia in the burrows of the mole rat (_Spalax_ _ehrenbergi_) decrease with increasing aridity due to a combination of low rainfall and lighter sandy soils.

Nonetheless, the Namib mole is precluded access to the large gaseous reservoir of a burrow system because of the soft shifting nature of the sand in which it lives. Although the good aeration properties of dry dune sand may prevent the development of low O_2 and high CO_2 tensions per se, the amount of oxygen available to the mole is limited by the physical constraint of withdrawing sufficient interstitial air from between sandgrains. The very low metabolic rate of E.g. namibensis is thus viewed as an adaptation to decrease gaseous exchange where the absolute amount of air available is limited by diffusion rates through sand.

This conclusion is supported by the experimental evidence of the present study. Although the relationship between VO_2 and ambient temperature for moles in sand was qualitatively similar to that for moles out of sand, metabolic heat production was significantly reduced in sand at ambient temperatures below 25°C. This indicates that the problem of extracting sufficient quantities of air from within sand limits the extent to which metabolic heat production can be increased at low ambient temperatures. Indeed, in sand at temperatures below 20°C, E.g. namibensis completely abandoned any attempt to thermoregulate. However, field measurements indicate that subsurface sand temperatures much below 20°C lie outside of those normally experienced by Namib moles.

Out of sand, E.g. namibensis was unable to sustain elevated levels of metabolism below 15^{o}C. Since moles are nocturnally active on the dune surface all year round (Chap. 4), air and sand surface temperatures below 15^{o}C may be encountered during winter (Lancaster, Lancaster & Seely, 1984). However moles usually restrict winter foraging activities to the warm early evening, while in summer they forage throughout the night (Chap. 4).

Cost of Burrowing and Habitat Productivity

The 'energy limitation hypothesis' of Vleck (1979, 1981) proposed that the high cost benefit ratio of burrowing and the resulting premium on energy conservation (especially in habitats of low productivity), is the primary factor selecting for low metabolic rates and small size in subterranean mammals.

The patchy and sparse distribution of prey resources in the Namib dunes has already been shown to have important implications for the foraging behaviour of the Namib mole (Chap. 2). The unusual physiological traits of this small dune insectivore may likewise be linked to minimisation of energy expenditure in response to scarce and widely dispersed food resources.

A metabolic rate that is 22% of that expected, would considerably reduce overall energy requirements of moles, and in conjunction with high rates of thermal conductance and small size, allow the use of low cost behavioural thermoregulation. Low metabolism and high thermal conductance in H. glaber are believed to be similarly involved (Jarvis, 1978). Namib moles exposed to a thermal gradient usually selected temperatures corresponding to those of their thermoneutral zone, thus enabling maintenance of high body temperatures with a minimum of energy expenditure. Measurements of summer sand temperatures indicate that physiologically optimal temperatures (30-36°C) are accessible day and night within the sand column at moderate depths. Thus it is possible at certain times of the year for E.g. namibensis to utilise behavioural thermoregulation, since moles can passively offload or gain heat when temperatures are lower or higher than preferred, by simply moving to depths which have favourable thermal conditions. Considering the close relationship found between sand and body temperature in wild caught moles, it is significant that individuals caught in summer generally exhibited body temperatures close to their preferred levels.

However, during winter, temperatures within the sand column may lie below the lower limit of thermoneutrality for moles during most of the day. Because of the small size and high rates of thermal conductance of E.g. namibensis, especially in sand, maintenance of only moderately high body temperatures requires a considerable increase in metabolic expenditure. Even at 20°C with a body temperature of 25°C, the resting metabolism of moles in sand had to be increased approximately threefold to that in thermoneutrality. As Lindstedt (1980a) and Bartholomew (1972) have pointed out, the high energy demands associated with thermoregulation often augment the problems inherent in environments where food availability is limited or fluctuating. Thus in energy sparse environments, natural selection will repeatedly favour the establishment of temporal patterns of energy utilisation such as torpor, which allow animals to reduce their energy expenditure (and thus their total demands for energy and water) as described for desert rodents (Buffenstein, 1985a; Withers, Louw & Henschel, 1980), shrews (Lindstedt, 1980a) and small insectivorous marsupials (Hume, 1982).

Maintenance of a low and labile Tb is qualitatively different from true torpor where body temperature is closely regulated during periods of activity and rapidly decreases to almost ambient during periods of reduced metabolism (Hudson, 1973; Hudson & Bartholomew, 1964). Most small mammals which use torpor, do so in response to food shortage and/or cold and maintain relatively precise homeothermy at all other times (Hudson, 1973). In contrast, E.g. namibensis, even when normally active had body temperatures as low as 27°C. This ability allows E.g. namibensis an increased activity range without the necessity for high energy expenditure to maintain a typical eutherian level of body temperature. A criterion distinguishing torpor from hypothermia is the ability of the animal to warm up by means of endogenous heat production (Hayden & Lindberg, 1970). Moles maintained in the laboratory at constant low temperature (±21°C) were able to rewarm spontaneously to body temperatures as high as 10°C above ambient, with arousal invariably occurring near to midday, and elevated temperatures being maintained till late evening. This daily cycle of rewarming seems consistent with the concept of a circadian clock (Nicoll, 1986) and qualitatively similar to the diurnal torpor employed routinely in the presence of adequate food in some other small mammals including small insectivorous marsupials (Dawson & Wolfers, 1978; Geiser, 1986; Morton & Lee, 1978), shrews (Frey & Vogel, 1978), rodents (Hill, 1975) and bats (Lyman, 1970).

Torpor in response to low ambient temperatures has been reported for _A_. _hottentotus_ (Korn, 1986; Kuyper, 1979). For this species, periods of torpor lasting three days were most frequently used for minimising energy expenditure. The indication of a circadian rhythm in torpor in _E_._g_. _namibensis_ begs the answer of its possible role under natural conditions.

The diel variation in body temperature in the laboratory independent of ambient is qualitatively similar to the rise and fall of body temperature of a mole kept in a bucket of sand exposed to the natural thermal fluctuations of the dune environment. In the laboratory, elevation of body temperature was achieved by internal heat production, whereas in the bucket buried in a dune, rewarming was facilitated by an external heat source. In both situations moles had elevated body temperatures to coincide with the start of nocturnal activity. It is suggested that during winter, when favourable sand temperatures are not always accessible, moles employ a daily cycle of torpor attuned to the daily warming and cooling pattern of the undersand environment. Field evidence lends support to this supposition.

In contrast to summer, winter caught moles excavated during mid-morning exhibited low body temperatures (19-25°C), reflecting the cool conditions in the sand column at this time. With the heating of the dune surface later on in the day, movement to shallower parts of the sand column would enable moles to employ energetically inexpensive passive means to elevate body temperatures for nocturnal foraging periods. Such behaviour can be considered analogous to the basking of the hyrax (*Procavia capensis*), whereby solar radiation is used to facilitate early-morning rewarming after nocturnal hypothermia (McNairn & Fairall, 1984). However, Robinson and Seely (1980) reported considerably cooler thermal conditions in winter (Ta=22.9°C at 20cm deep) than those measured in this study. Under these circumstances, moles would have to place increased reliance on internal heat production for elevation of body temperatures to levels sufficiently high to enable evening activity.

CONCLUSIONS

The unusual metabolic traits of *E.g. namibensis* greatly exaggerate physiological trends found in most other subterranean mammals, including other chrysochlorids. The extremely low metabolic rate and resulting thermolability of *E.g. namibensis* are not viewed as a manifestation of a primitive phylogeny but rather as adaptations to fossoriality in an energy sparse and arid sand dune environment. Tolerance of stressful temperatures is affected primarily by behavioural rather than physiological means i.e. nocturnal activity and selection of favourable microclimates within the sand column. For these reasons, largely non-thermoregulatory determinants are suggested as selecting for the physiological traits of *E.g. namibensis*. A low metabolic rate is of advantage in an undersand environment where gaseous exchange is limited. Furthermore, a low metabolic rate reduces energy expenditure, and together with high thermal conductance and small size, enables the utilisation of low cost behavioural thermoregulation. Employment of diurnal torpor may be an additional energy saving mechanism associated with seasonal changes in the thermal regime of the undersand environment.

CHAPTER 6

WATER METABOLISM

INTRODUCTION

Free water is usually not available in arid and semi-arid environments, thus the ability to exist without drinking water is a prerequisite for the survival of small desert mammals. According to Gettinger (1984b), the term 'water independent' applies primarily to granivorous rodents that can exist on a dry seed diet with no exogenous free water (Hinds & MacMillen, 1985; Koford, 1968; MacMillen & Lee, 1969). Water dependent species must supplement metabolic water with preformed water and achieve water economy through utilisation of moist food resources such as insects or green vegetation (Bradford, 1974; Degen, Kam , Hazan & Nagy, 1986; Karasov, 1983; Mares, 1977).

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

The present study examines the validity of the above premise with regard to the Namib Desert golden mole, *Eremitalpa granti namibensis*, a small insectivore inhabiting an energy sparse sand dune environment where rainfall is irregular and unreliable (Lancaster, Lancaster & Seely, 1984). Namib moles are nocturnally active on the dune surface searching for insect prey, while daylight hours are spent buried in loose shifting dune sand. In a combination of laboratory feeding trials and field studies of energy and water metabolism using tritiated water, I examined the ability of *E.g. namibensis* to survive on an insect food resource without drinking water, the coupling of energy and water expenditure and the magnitude of energy and water requirements. Since adjustments of renal output are one of the major physiological responses a mammal may make to remain in water balance (MacMillen 1972), urine concentrating ability and kidney structure were also investigated. It was hoped that this approach would elucidate the relationship between water metabolism, energy metabolism and physiological adaptation to the arid sand dune environment of *E.g. namibensis*.

MATERIALS AND METHODS

Gravimetric Determinations of Energy and Water Balance

Adult moles (five females; two males) were housed individually in (30x24x24cm) glass terraria filled to a 15cm depth with Namib dune sand. Terraria were kept in a constant environment cabinet maintained at an ambient temperature of 29°C, 50% relative humidity and a 12 hour photoperiod with illumination from 07h00 - 19h00. A four day acclimation period preceded commencement of any measurements. During the ten day test period, animals were weighed and fed daily at 17h00 with mealworms (*Tenebrio molitor* larvae) *ad lib*.. All excess larvae and exuvia from the previous day were collected by sieving the sand in each tank, and daily food consumption (to the nearest 0.01g wet mass) measured as the difference between the mass of larvae supplied and those left unconsumed. No free drinking water was supplied. Control samples of larvae were not monitored since loss in mass for periods longer than 24 hours is negligible even after pupation (Hawkins & Jewell, 1966).

To avoid contamination with sand, urine and faecal production were measured by placing moles in metabolic cages (19 x 12 x 12cm) for six hour periods at different times during the 24 hour cycle. A stainless steel tray filled with mineral oil and covered by a fine wire mesh (0.04cm^2) was suspended beneath the wire grid floor of the metabolic cage. Faeces were trapped on the wire mesh whereas urine fell through and collected under the mineral oil. MacMillen and Lee (1969) reported neither loss nor gain of water to or from mineral oil during periods of collection and storage of urine samples. Volumes of urine produced for each six hour sampling period were measured using a 0.5ml graduated syringe. Osmolality of urine samples was measured with an Osmomat 030 cryoscopic osmometer. All faecal material collected was dried at 50°C to constant mass and then weighed to the nearest 0.01g. The energy content of food and faeces was measured by microbomb calorimetry. Each mole was subjected to eight collection periods (48 hours in total) spread evenly through the ten day experimental period. Since no significant difference was observed either for urine (one-way anova: F=2.61; p>0.05; d.f.=3,29) or faecal production (one-way anova: F=0.17; p>0.05; d.f.=3.29) at different times of the day-night cycle, daily production per animal was calculated using the average amount produced per six hour period times four.

Calculation of energy expenditure

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

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

where: DEI is daily energy intake; GEI is gross energy intake calculated as energy content of food x mass of food consumed per day; FE is energy lost in faecal matter calculated as energy content of faeces x mass of faeces produced per day; UE is energy content of urine. Urine energy was not considered in these calculations because it constitutes a negligible fraction of energy exchange in small mammals (Grodzinski & Wunder, 1975). Since moles maintained relatively stable mass (mass change <3.5%; Fig. 6.1) during the period of measurement, daily energy expenditure (DEE) was assumed to be equal to DEI, and representing only respiration required for body maintenance and activity (Drodz, 1975; Gessaman, 1973).

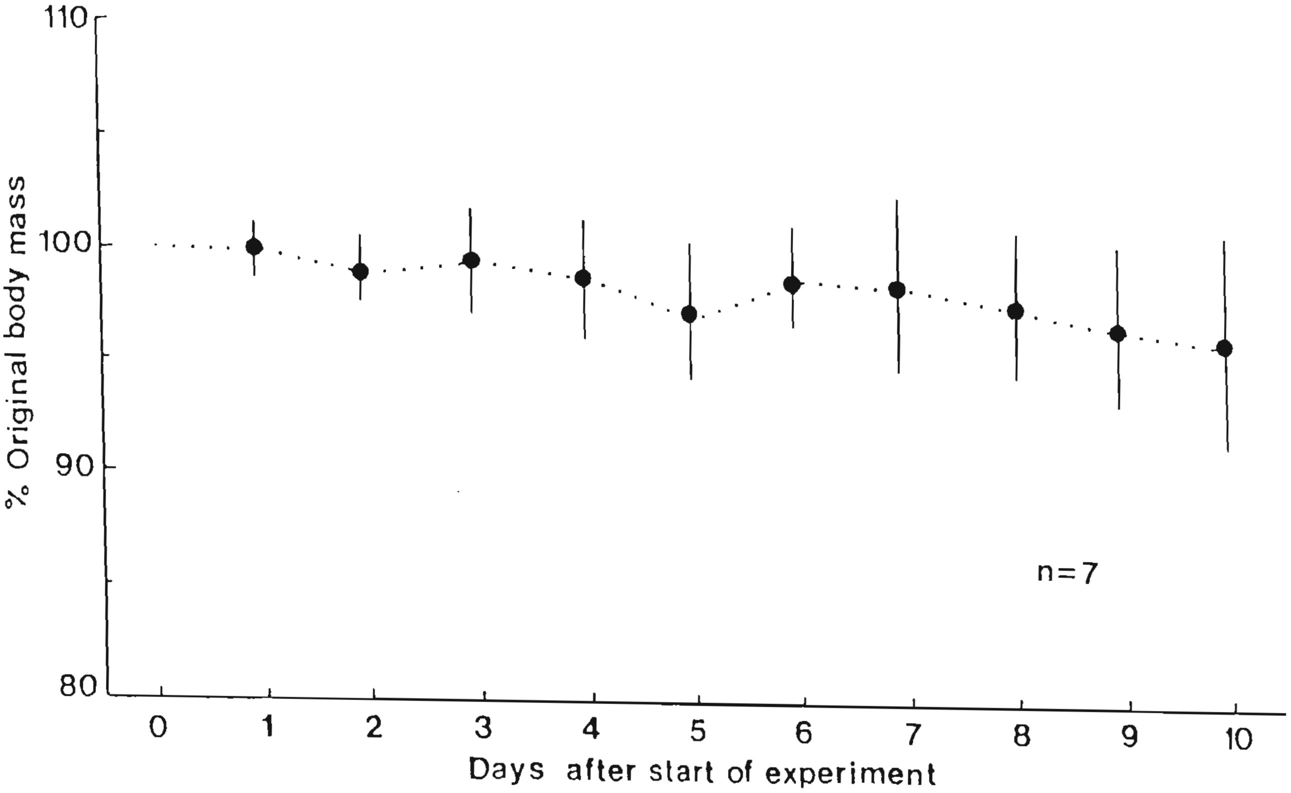

FIGURE 6.1: Changes in body mass for _E.g._ _namibensis_ on a diet of mealworms with no drinking water. Results expressed as the mean ± 1 S.D..

'Apparent assimilation efficiency' (AE) was calculated from the daily energy intake (DEI) and the gross energy intake (GEI) (Grodzinski & Wunder, 1975):

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

Calculation of water balance

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

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

Water intake. D is amount of water drunk, and was not considered in these calculations since no water was supplied to test animals. P is preformed water in food, calculated as the difference in mass after oven-drying mealworms at 50°C to constant mass. M is metabolic water production from oxidation of food calculated by using the following conversion constants: protein - 0.39ml g^{-1}food; carbohydrate - 0.56ml g^{-1}food; fat -1.07ml g^{-1}food (Schmidt-Nielsen, 1979) (Table 6.1) and taking into consideration AE to account for metabolic water loss in egesta. Hence daily intake of preformed and metabolic water were calculated from daily food consumption.

Water loss. U is daily urinary water loss. F is daily faecal water loss calculated from daily faecal production. Since moles rarely defaecated during handling, water content of freshly voided faeces was not determined. Instead, faeces were collected at one hour intervals from animals in metabolic

TABLE 6.1: Food values of Tenebrio molitor larvae supplied to captive E.g. namibensis

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

Energy 25.02 kJ g^{-1} ash free dry mass

Preformed water 62.1%

chambers and water content calculated as the difference in mass after oven drying at 50^{o}C to constant mass. Hulbert and Dawson (1974b) found that for bandicoots, the error involved in determining faecal water content was never more than 10% when fresh faeces were compared with faeces left for 12 hours. EWL is pulmocutaneous water loss determined indirectly from the subtraction of daily faecal and urinary water loss from water intake.

Water Turnover Determinations Using Tritiated Water (^{3}HHO)

Theoretical considerations

Tritium is a radioactive isotope of hydrogen which has become increasingly popular in recent years as a tool for measuring water flux in both captive and free-ranging animals. Pinson (1952) has outlined the favourable characteristics of tritium for use in biological experimentation which include a half life of 12 to 13 years and a low radiological working hazard since radioactive decay is in the form of soft beta particles rather than the more harmful gamma radiation.

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

Validation trials

The precision of isotope measurement of water flux was assessed by comparing water influx measured gravimetrically with the isotopic measurement. During the experimental period, seven adult moles (five females; two males) were maintained at 29°C, under similar conditions to those described previously for energy and water balance determinations. Mealworms were supplied ad lib. but no drinking water was provided. A three day acclimation period was allowed prior to injecting moles intraperitoneally with ^{3}HHO (0.05mCi in 0.5ml sterile water). After a three hour equilibration period to allow isotopically-labelled water to come into equilibrium with body water (Mullen, 1970; Holleman & Dieterich, 1973), a first blood sample was collected by toe clipping and a second sample taken by the same technique ten days later. Blood samples (±0.1ml) were stored at 4°C in 500µl plastic micro-centrifuge tubes sealed with beeswax until further analysis. During the ten day test period, daily food consumption was monitored enabling simultaneous measurements of water flux by both gravimetric and isotopic methods.

Measurement of water turnover rates in the field

All field studies were conducted in the dunes near to Gobabeb from 4th to 20th March 1987. Mean daily temperature extremes were 31.9°C and 13.8°C and mean daily extremes of relative humidity were 84.9% and 29.5%. No rainfall occurred but fog precipitation was 2.0ml. Animals were caught between 07h00 and 10h00 either by hand or by pitfall trap and taken to the field station at Gobabeb for processing. Moles were weighed and sexed prior to administration of 0.05mCi ^{3}HHO in 0.5ml sterile water by intraperitoneal injection. Initial blood samples were collected by toe clipping after a three hour equilibration period and animals returned to their exact site of capture and released (between 18h00 and 19h00). Of ten moles released, five (all female) were recaptured 9-15 days later, reweighed, and a second blood sample collected by toe clipping. All blood samples were stored, as described previously, for three months.

Processing of blood samples

Extraction of water from blood samples involved vacuum sublimation in liquid nitrogen using the method of Vaughan and Boling (1961). Extracted water was stored in sealed 200 µl plastic micro-centrifuge tubes at 4°C until measurement of radioactivity one month later.

Radioactivity of extracted water was measured by diluting 20 µl amounts in 5ml of Beckman Premixed-Ready-Solv HP/b scintillation fluid. Samples were counted for two minutes on a Beckman LS 3801 scintillation counter. Count accuracy was to 2% error and was corrected for background. Since all samples were counted at the same time, no correction factor was necessary for radio isotope decay (Green & Dunsmore, 1978; Nagy, 1972).

Calculations

Water flux rates were calculated using equation three of Nagy and Costa (1980).

$$\frac{\text{ml } H_2O \text{ flux}}{\text{kg day}} = \frac{1000W \ln(H_1/H_2)}{Mt}$$

where H_1 and H_2 are tritium values in CPM (counts per minute) for initial and final blood plasma samples, W is total body water in ml (see below), M is body mass in g, t is days between blood samples and ln is natural logarithm. Since under normal physiological conditions, the animal is in water balance, the above equation describes both rate of water gain and water loss.

Fat and water content determinations

Total body water content of moles (eight laboratory maintained individuals that had died of natural causes and 14 wild caught moles) was determined by oven drying fresh carcasses (with gut removed) to constant mass at 50°C. Difference in mass between dried and fresh carcasses was taken as representing total body water. Tritium dilution procedures for estimating body water volumes (Yousef *et al*., 1974) were not used in final calculations since these procedures may overestimate water content by as much as 10% (Gettinger, 1983; Green & Eberhard, 1983; Karasov, 1983; Nagy, Seymour, Lee & Braithwaite, 1978).

Dried carcasses were finely ground in a coffee grinder and extracted to constant mass with petroleum ether in a Soxhlet apparatus to determine fat content according to the method of Allen, Grimshaw, Parkinson and Quarmby (1974) and Sawicha-Kapusta (1975).

Kidney Morphology

Kidneys removed from two freshly-killed laboratory maintained animals were fixed in Bouin's solution for 72 hours, embedded in paraffin wax and sections cut at 10 μm. The Masson trichome staining method was employed (Culling, 1974). Sections corresponding to the midsagittal section of the kidney were photographed under a binocular microscope (6-12x magnification) and the resulting photomicrograph enlarged to 20x16cm. The outline of the kidney was traced onto $1mm^2$ graph paper and the number of squares occupied by the cortex and the medulla recorded. Relative medullary area (RMA) was calculated as medullary area/cortical area (Brownfield & Wunder, 1976).

For comparative purposes, RMA of kidneys from two Amblysomus hottentotus caught at Umdoni Park, Natal, was determined using the same procedure.

RESULTS

Laboratory Determinations of Energy and Water Balance

A complete account of energy and water balance for E.g. namibensis is shown in Table 6.2 and Table 6.3 respectively. Moles maintained water balance and body mass on a mealworm diet in the absence of drinking water. The rate of fresh food consumption while maintaining body mass was low at about

TABLE 6.2: Energy budget of _E.g._ _namibensis_ fed _Tenebrio_ _molitor_ larvae in the laboratory

	Mean	± 1 S.D.
No. of animals	7	
Mass (g)	27.29	6.93
Food consumption ($g.day^{-1}$)[a]	1.22	0.34
Faecal production ($g.day^{-1}$)[a]	0.48	0.12
Energy content of faeces (KJg^{-1})[a]	10.35	1.62
GEI (KJ day^{-1})	30.61	8.46
Faecal energy (KJ day^{-1})	4.77	0.88
DEE (KJ day^{-1})	25.84	8.25
% predicted DEE[b]	54.10	14.47
Apparent assimilation efficiency (%)	83.34	5.38

[a] Data are expressed per gram dry mass.

[b] Calculated from Grodzinski and Wunder's (1975) equation for an insectivore, converted to KJ ($1cm^3 O_2$=0.02KJ: Schmidt-Nielsen, 1979) and corrected for temperature according to Randolph (1980).

Predicted DEE at 29°C ($KJg^{-1}day^{-1}$)=$12.92W^{-0.50}-(0.37W^{-0.46})9$ where W=body mass in g.

TABLE 6.3: Water budget of *E.g. namibensis* fed *Tenebrio molitor* larvae in the laboratory with no drinking water supplied

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

14% of body mass each day, while daily energy expenditure was much less than that predicted by mass. High assimilation efficiencies reflected the low chitin content of the food supplied. The major avenue of water loss was pulmocutaneous accounting for 76% of the total loss. Faecal water loss was the second most important avenue (13%), and water loss in the urine the least (11%). Mean urine osmolality was 3.82 osmol kg^{-1} (S.D.±1.00). The ratio of energy to water turnover (WTR/DEE : $mlH_2O\ KJ^{-1}$) was calculated as 0.10 $mlKJ^{-1}$.

Kidney Morphology

The gross kidney morphology of A. hottentotus and E.g. namibensis is shown in Fig. 6.2. Both species, according to the classification of Sperber (1944) possessed simple kidneys with a single papilla. In E.g. namibensis the renal papilla was elongate extending well down into the ureter. Relative medullary area was 1.64 for E.g. namibensis and 1.10 for A. hottentotus.

Body Composition

A comparison of the water and fat contents of wild and captive moles is presented in Table 6.4. The two groups showed no difference in percentage fat content but body water as a percentage of total body mass and lean body mass was significantly lower in laboratory maintained individuals. Since the disparity in body water did not reflect differences in fat stores, body water turnover comparisons were made on the basis of total body mass assuming a mean water content of 49.61% for captive moles and 59.88% for wild moles.

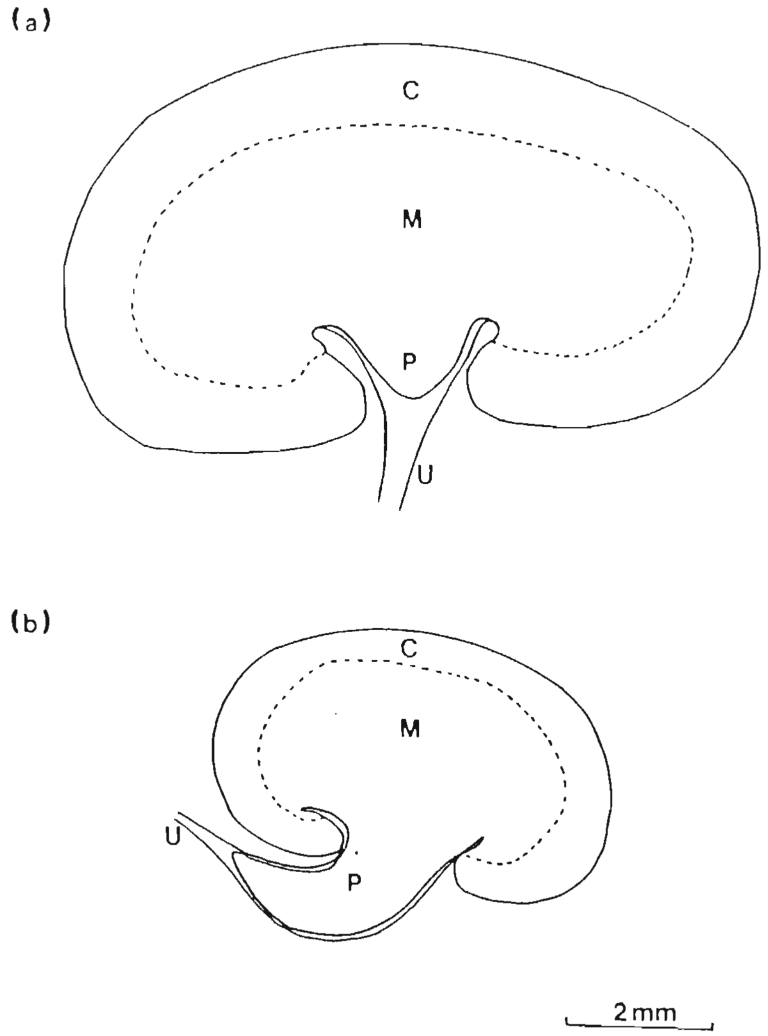

FIGURE 6.2: Cross section of the kidney showing the cortex (C), medulla (M) form of the papilla (P) and ureter (U): (a) *A. hottentotus*; (b) *E.g.namibensis*.

TABLE 6.4: Body composition of wild caught and laboratory maintained E.g. namibensis. Results expressed as mean (± 1 S.D.)

	Laboratory		Field		Sig.[a]
No. of animals	8		14		
Body mass (g)	18.69	(2.61)	20.17	(4.21)	-
Total body water (g)	9.17	(1.96)	12.18	(2.99)	-
% Water content[b]	49.61	(9.84)	59.88	(5.81)	$p<0.01$
Total body fat (g)	2.94	(1.96)	2.00	(0.88)	-
% Fat content[c]	28.28	(11.15)	23.71	(6.46)	NS
Lean body mass (g)	15.50	(1.84)	18.17	(3.61)	-
TBW/LBW[d]	58.07	(7.53)	66.39	(5.40)	$p<0.02$

[a] Student's t-test (after arc-sin transformation):
NS=not significant

[b] Expressed as percentage of total wet body mass

[c] Expressed as percentage of dry body mass

[d] (Total body water/lean body weight) x 100

Validation Trials

Water flux measured by isotopic dilution showed a strong positive correlation with gravimetric determinations (Fig. 6.3), and in seven paired comparisons, no significant difference was observed between the two measurements (paired t-test: $t=1.17$; $p>0.05$; d.f.=6). Although no consistent trend was apparent, mean turnover rates based on tritium dilution were 6.23ml kg^{-1}day, 6.7% higher than estimates based on food consumption analysis (Table 6.5).

Tritiated Water Turnover in Free-living and Laboratory Maintained Animals

Isotopically determined water turnover of free-living *E.g. namibensis* was significantly lower than that of animals maintained in the laboratory at 29°C with food provided *ad lib*. but no water (Student's t-test: $t=2.50$; $p<0.05$; d.f.=10) (Table 6.6). The mean water flux of wild animals was 23% lower than that measured in the laboratory.

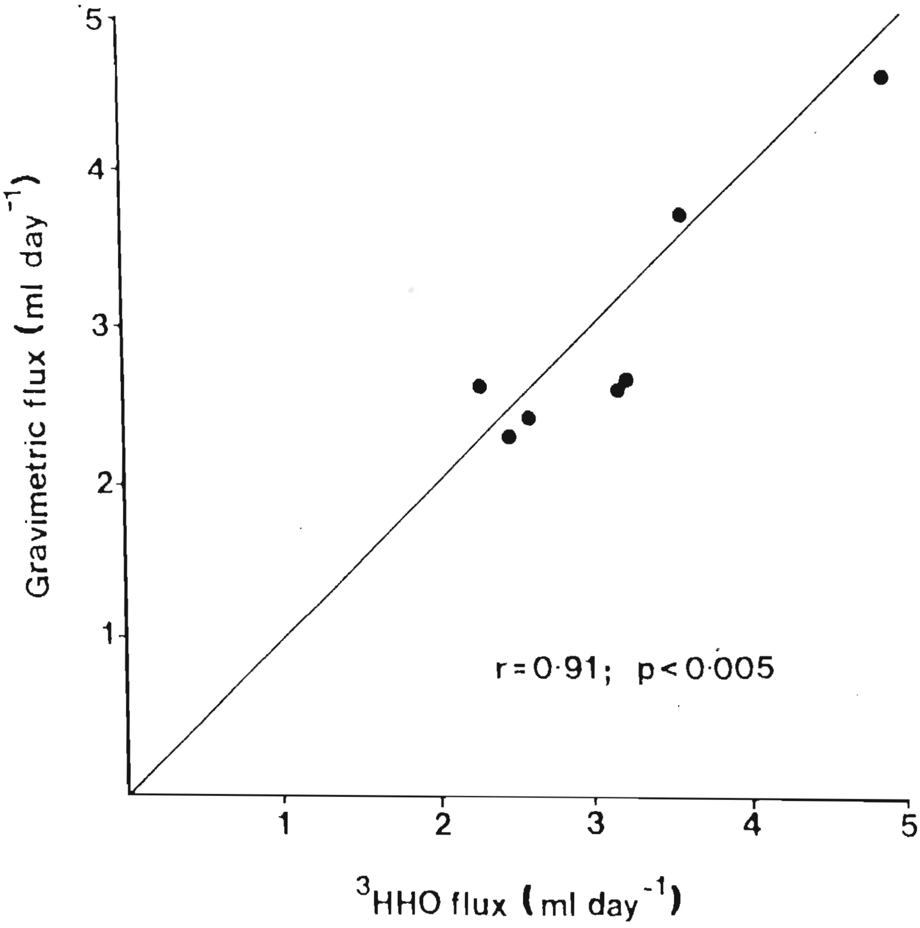

FIGURE 6.3: Comparison of gravimetric and isotopic water turnover in E.g. namibensis. Solid line represents a 1:1 relationship.

TABLE 6.5 A comparison of water influx determined from tritiated water turnover (^{3}HHO) and by gravimetric measurement, over a ten day period

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

[a] Calculated as 100 (^{3}HHO value-gravimetric value/gravimetric value)

TABLE 6.6: A comparison of tritiated water turnover in free-living and laboratory maintained E.g. namibensis. Results expressed as the mean (± 1 S.D.)

	Free-living		Laboratory	
No. of animals	5		7	
Period of measurement (days)	9-15		10	
Body mass (g)	19.76	(2.68)	27.66	(4.93)
Water turnover(ml kg-1 day-1)	87.64[a]	(20.07)	113.87[b]	(12.45)

[a] Calculated assuming 59.88% body water content

[b] Calculated assuming 49.61% body water content

DISCUSSION

Interrelation of Water Turnover Rate and Daily Energy Expenditure

The turnover rates of energy and water in mammals are biologically linked (Lifson & McClintock, 1966) and some correlation has been found between ad lib. water intake and resting energy expenditure of ruminants (Macfarlane & Howard, 1972), rodents (Mullen, 1970; Yousef et al., 1974) and marsupials (Kennedy & Macfarlane, 1971). However, Withers, Louw and Henschel (1980) criticised the approach of previous workers and proposed that rates of water usage should be examined in relation to daily energy expenditure rather than resting rates of oxygen consumption. They add that for arid dwelling mammals which seldom have access to free water, water turnover rate and daily energy expenditure must be coupled through diet and assimilation efficiency (since water turnover rate = preformed water + metabolic water = water intake = water loss for steady state conditions).

The available data on granivorous desert rodents indicate that there is a similar low ratio of water to daily energy expenditure (WTR/DEE) of about 0.04 $\mathrm{ml H_2O\ KJ^{-1}}$ (Withers et al. 1980), which is considerably less than the 0.10ml $\mathrm{H_2O\ KJ^{-1}}$ calculated for E.g. namibensis. Unfortunately there are no comparable data for insectivorous species despite the potential of laboratory feeding trial experiments to simultaneously measure water and energy requirements. Nevertheless, insectivores fed on fresh meat or insects have comparable assimilation efficiencies to E.g. namibensis (Barrett & Stueck, 1976; Churchfield, 1982; Hanski, 1984; Jensen, 1983) and can be expected to show a similar WTR/DEE ratio in the absence of free drinking water.

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

Morton (1980) argued that in nocturnal arid dwelling insectivorous animals there is little evidence of adaptation to reduced water supply, since behavioural avoidance of stressful temperatures through nocturnalism and fossoriality together with the high water content of an insect diet, effectively removes the physiological problem of water conservation. Consequently, in the absence of selection for conservation of water, the pattern of water usage is a direct reflection of the energy turnover rate of the animal.

A major problem facing E.g. namibensis is a sparse and patchily distributed food resource (Chap. 2), thus a low daily energy expenditure is viewed primarily as of adaptive significance to survival in an energy sparse environment.

Considering the coupling between energy and water usage, low rates of energy turnover in the Namib mole result in a concomitant although perhaps coincidental reduction in water requirements. Indeed, water turnover rate of E.g. namibensis is amongst the lowest recorded for insectivorous species measured under similar experimental conditions (Table 6.7).

Water Independence in Relation to Kidney Function

The present study has demonstrated that E.g. namibensis is independent of drinking water when fed on a mealworm diet containing 62% water content. Free-living Namib moles feed predominantly on termites and insect larvae which have water contents ranging from 63% to 80% (Chap. 2; Redford & Dorea, 1984). It is probable, therefore, that E.g. namibensis can always obtain sufficient water from its food provided that excess water expenditure on heat dissipation is avoided. Nocturnal and burrowing habits in Namib moles preclude exposure to rigorous diurnal surface conditions. Other nocturnal desert dwelling insectivorous animals known to be capable of subsisting without drinking water on a diet of fresh meat or insects include dasyurid marsupials (Haines et al., 1974; Morton, 1980) shrews (Lindstedt, 1980b), armadillos (Greegor, 1975), rodents (Schmidt-Nielsen & Haines, 1964; Whitford & Conley, 1971) and hedgehogs (Yaakobi & Shkolnik, 1974).

Although an insect diet has a high moisture content and hence provides more water than an energetically equivalent diet of

TABLE 6.7: Rates of water turnover in small insectivorous mammals in the laboratory with minimum water requirements

Species	Mass(g)	ml day^{-1}	ml kg$^{-0.82}$ day^{-1} [b]	Reference
Macrotus lagotis[a]	1081	31.60	33.16	Hulbert & Dawson 1974
Isoodon macrourus	1468	40.90	35.68	Hulbert & Dawson 1974
Perameles nasuta	972	38.90	45.01	Hulbert & Dawson 1974
Eremitalpa granti namibensis[a]	27.3	2.70	51.73	This study
Dasyuroides byrnei[a]	127	10.00	57.75	Haines *et al*. 1974
Antechinus stuarti	25.8	7.63	153.00	Nagy *et al*. 1978
Sminthopsis crassicaudata[a]	14.9	5.03	164.70	Morton 1980
Blarina brevicauda	23.1	9.40	247.76	Deavers & Hudson 1979

[a] Arid dwelling

[b] All water turnover rates standardised to correct for differences in body mass using the exponent 0.82 (Macfarlane & Howard, 1972).

seeds (Linstedt, 1980b), the high protein intake of an insect diet involves the liability of considerable nitrogenous wastes (Schmidt-Nielsen & Newsome, 1962). In mammals, nitrogenous wastes from protein catabolism must be excreted in urine primarily as urea. Consequently urinary water losses from an insect diet exceed those of a seed diet (Linstedt, 1980b). In some instances the additional water in an insect diet does not compensate for the increased urinary water loss. Certain species of desert insectivorous bats are unable to achieve water balance on an insect diet alone and require free drinking water to maintain circulation and excretion (Carpenter, 1969; Geluso, 1978). The success of these animals in arid environments is by virtue of their ability to fly long distances to free water sources.

Thus, contrary to Morton's (1980) arguments, a physiological factor that may limit survival of insectivorous mammals in arid environments is the capacity to excrete large quantities of urea in small volumes of urine. An examination of urinary concentrating abilities of small insectivorous mammals during water deprivation supports this conclusion (Table 6.8). Although there is some overlap, desert species including *E.g. namibensis* generally produce more concentrated urine (2300-4300 mmosmol kg^{-1}) than mesic inhabiting species (1800-3000 mmosmol kg^{-1}). Even so, urine concentrating capacities of desert insectivores are not remarkable in comparison to those of granivorous desert rodents.

In the Namib mole, production of a concentrated urine reduced

TABLE 6.8: Mean osmotic concentrations of the urine of mammals in the laboratory during water restriction

Species	Urine osmolality (mosmol kg^{-1})	Reference
Insectivorous arid zone		
Pipistrellus hesperus	4340	Geluso 1978
Hemiechinus auritus	4010	Yaakobi & Shkolnik 1974
Antrozous pallidus	3980	Geluso 1975
Eremitalpa granti namibensis	3820	This study
Paraechinus aethiopicus	3634	Yaakobi & Shkolnik 1974
Macrotis lagotis	3566	Hulbert & Dawson 1974
Onychomys torridus	3180	Schmidt-Nielsen & Haines 1964
Sminthopsis crassicaudata	2322	Morton 1980
Insectivorous mesic zone		
Erinaceus europaeus	3062	Yaakobi & Shkolnik 1974
Isoodon macrourus	2942	Hulbert & Dawson 1974
Myotis volans	2910	Geluso 1978
Planigale maculata	2317	Morton 1980
Blarina brevicauda	1820	Deavers & Hudson 1979
Granivorous arid zone		
Notomys alexis	6547	MacMillen & Lee 1969
Desmodillus auricularis	5507	Buffenstein 1985b
Leggadina hermannsburgensis	4711	MacMillen *et al*. 1972
Gerbillus pusillus	4084	Buffenstein 1985b
Liomys salvini	4000	Hudson & Rummel 1966

water loss via this avenue to only 11% of the total. Similar contributions have been reported for other desert insectivores (Hulbert & Dawson, 1974; Whitford & Conley, 1971). In contrast, urination in the mesic dwelling shrew, Blarina brevicauda (Deavers & Hudson, 1979) and the dasyurid marsupial, Antechinus stuartii (Nagy et al., 1978) accounts for 34% and 20% respectively of the total water loss on a water restricted diet.

A complete lack of information on the water metabolism of the African golden moles (Chrysochloridae) makes it difficult to decide whether efficient kidney function in E.g. namibensis represents a specific adaptation to an arid environment, or whether this physiological attribute is a general characteristic of the family.

It has long been accepted that gross kidney morphology is a reliable indicator of urinary concentrating capacity (Sperber, 1944; Schmidt-Nielsen & O'Dell, 1961). Those mammals with greater kidney concentrating ability often have elongate renal papillae and more prominent medullae than animals with lesser abilities. Various renal indices have been proposed to estimate urine concentrating capacities (see Brownfield & Wunder, 1976 for review). Those involving medullary area such as used in this study, have been found to be more strongly correlated with and thus better estimators of renal performance than ones utilising medullary thickness. The data of Brownfield and Wunder (1976) yield the following predictive equation:

$$\text{Maximum urine concentration (mosmol kg}^{-1}\text{)} = 837 + 2106.\text{RMA}$$

where RMA is relative medullary area. The predicted maximum concentration of the urine of the Namib mole is 4300 mosmol kg^{-1}, a value higher than laboratory determinations indicating that experimental conditions were not sufficiently stressful to elicit the maximum concentrating potential. Predicted maximum for the Hottentot golden mole was 3200 mosmol kg^{-1}. These findings are consistent with the ecological distribution of these two species with _E.g._ _namibensis_ having kidneys better adapted for water conservation than the mesic zone _A. hottentotus_. Similar relationships have been found in bats (Geluso, 1978), shrews (Lindstedt, 1980b), rodents (Heisinger, King, Halling & Fields, 1973), peramaloid marsupials (Hulbert & Dawson, 1974b), hedgehogs (Yaakobi & Shkolnik, 1974) and armadillos (Greegor, 1975).

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

Validation of the ^{3}HHO Technique

Water and energy balances established under laboratory conditions, although providing useful insight into energy and water requirements as well as the mechanisms involved in water conservation, may be very different when obtained on free-living animals (Bradford, 1974; Grubbs, 1980; Grenot, Pascal, Bascarlet, Francas & Sellami, 1984). Measurements of water flux in free-living moles using ^{3}HHO were aimed primarily towards investigating the impact of biological and environmental factors on water and energy economy. Such studies, however, demanded an evaluation of the precision of isotopic dilution methodology for estimating body water turnover in _E.g._ _namibensis_.

Use of the ^{3}HHO method to measure water turnover is based on the following assumptions (Lifson & McClintock, 1966; Nagy & Costa, 1980; Gettinger, 1983):

1. Body mass and total body water remain constant.
2. Influx and efflux rates of water remain constant.
3. All the body water is uniformly labelled and there is no incorporation of labelled hydrogen into other body constituents. Furthermore, water is the only form in which the hydrogen of the body water is lost.
4. The specific activity of hydrogen of water lost from the body is equal to that of the body water.
5. No water (labelled or unlabelled) enters the body with inspired air or through the skin.

Several workers have stressed that under almost any conditions the above assumptions are violated to some extent (Lifson &

McClintock, 1966; Mullen, 1971; Nagy & Costa, 1980), resulting in either over or underestimates of water flux in comparison to gravimetric determinations. Several validation studies have confirmed this conclusion with reported errors ranging from 37% (Grenot et al., 1984) to 5% and less (Gettinger, 1983; Green & Dunsmore, 1978; Grubbs, 1980; Karasov, 1983). In burrowing and fossorial animals, violation of assumption five is especially troublesome (Gettinger, 1983; Mullen, 1971). Burrows are often humid (Kennerly, 1964) hence animals inhabiting such environments will receive a considerable input of water vapour. Similarly, within the confined microenvironment around a mole resting submerged in sand, accumulation of water vapour from respiratory surfaces and excreta may reach near saturation levels.

Nagy and Costa (1980) investigated errors due to tritium measured influx rate in Kangaroo rats (*Dipodomys merriami*) living in artificial burrows in dry and moist soil, and found that ^3H in water vapour lost from the animal, rapidly exchanged with unlabelled soil water even in relatively dry soil. They concluded that water flux measurements in burrowing and fossorial mammals are more likely to include overestimates due to unlabelled vapour influx than underestimates resulting from labelled vapour influx. Overestimates due to unlabelled influx can result in errors of up to 52% and 20% in moist and dry burrows respectively (Nagy & Costa, 1980).

In laboratory validation trials for _E.g._ _namibensis_ tritiated water turnover was strongly correlated with and did not differ significantly from actual water turnover. However five out of seven isotopically determined measurements overestimated actual water flux (error 3-25%) indicating that unlabelled water vapour influx introduced some error into calculations of turnover rates. Similar overestimations can be expected for free-living animals which spend much of the day buried in dune sand. Since water flux rates were not consistently overestimated by isotope turnover, a second major source of error could have arisen from violation of the assumption that all test animals had a total body water content of 49.6%. Underestimates of body water would result in underestimates of water flux and vice versa. If all test animals had been sacrificed after completion of validation trials to enable individual determinations of body water contents, more accurate measurements may have been obtained. Due to scarcity of moles for future experimental work, this approach was not feasible. Thus tritiated water turnover (as it was measured here) appears useful as an index, but does not measure water turnover _per_ _se_.

For free-living animals, a constant body water content of 59.9% was assumed. The reason for higher water contents in wild moles is not known since no difference in fat content was apparent between wild and laboratory maintained individuals. Other workers have likewise reported higher water contents in wild animals in comparison to captive individuals but have attributed the difference to accumulation of excess fat in captivity (Churchfield, 1981; Holleman, White & Feist, 1982; Richmond, Trujillo & Martin, 1960).

Water and Energy Flux in the Field

Water fluxes of desert insectivores in their natural habitat are typically higher than minimum water turnover rates measured in the laboratory (Hulbert & Dawson, 1974a; Hulbert & Gordon, 1972; Morton, 1980). Higher rates in the field reflect the extra metabolic and food demands of a free and active life and sometimes the intake of free water (Morton, 1980). In contrast *E.g. namibensis* had a significantly lower water turnover rate in the field than in the laboratory. Indeed, water flux of free-living Namib moles is amongst the lowest recorded for small desert mammals with the exception of some granivorous rodents and the herbivore rodent *Petromus typicus* (Table 6.9). Low rates of water usage in Namib moles indicate that the physiological and behavioural attributes of this species which restrict water turnover (i.e. efficient kidney function, low rates of energy usage, nocturnalism and burrowing habits) are of adaptive value to field populations.

Whether the relative contributions of the different avenues of water intake were the same in the wild as in the laboratory is unknown. Condensed fog water provides a supplementary source of drinking water for many Namib dune animals (Hamilton & Seely, 1976; Louw, 1974; Louw & Holm, 1972; Seely & Hamilton, 1976) and fog precipitation did occur during the measurement

TABLE 6.9: Rates of water turnover in free-living desert dwelling small mammals measured by isotopic dilution methods

Species	Mass(g)	Water flux[a]		Reference
		ml day^{-1}	ml kg$^{-0.82}$day^{-1}	
Insectivorous				
Eremitalpa granti namibensis	19.8	1.73	43.13	This study
Macrotis californicus	12.9	2.46	87.14	Bell *et al*. 1986
Isodon macrourus	873	103.01	115.15	Hulbert & Gordon 1972
Sminthopsis crassicaudata	15.0	16.47	398.00	Morton 1980
Herbivorous				
Petromus typicus	130.0	5.07	27.00	Withers *et al*. 1980
Thomomys bottae	99.4	25.45	169.00	Gettinger 1984
Omnivorous				
Acomys missatus	45.0	5.65	71.79	Degen *et al*. 1986
Acomys cahirinus	38.3	5.04	73.20	Degen *et al*. 1986
Sekeetamys calurus	41.2	5.89	80.47	Degen *et al*. 1986
Pseudomys albocinerius	20.2	3.31	81.20	Morris & Bradshaw 1981
Meriones libycus	59.6	8.70	86.00	Lachiever *et al*. 1974
Meriones shawii	78.0	11.10	90.00	Lachiever *et al*. 1974
Granivorous				
Perognathus formosus	16.0	1.12	33.25	Mullen 1970
Petromyscus collinus	19.0	1.41	36.30	Withers *et al*. 1980
Aethomys namaquensis	46.0	3.22	40.20	Withers *et al*. 1980
Dipodomys microps	55.0	6.05	65.30	Mullen 1971
Dipodomys merriami	31.0	4.03	69.60	Mullen 1971

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[a] All water turnover rates standardised to correct for differences in body mass using the exponent 0.82 (Macfarlane & Howard, 1972).

period of water turnover. However, it is significant that the distribution of E.g. namibensis is not confined to the Namib fog belt as for Bitis peringueyi and Aporosaura anchietae, two reptiles which make regular use of condensing fog water (Louw, 1972). Furthermore water provided to laboratory maintained animals in a shallow petri dish was always ignored, whereas other golden moles and talpid moles drink freely in captivity (Kuyper, 1979; MacDougal, 1942; Mellanby, 1967). These observations suggest that Namib moles do not usually utilise free water but rely solely on dietary water intake to satisfy their needs.

For animals that obtain moisture exclusively from their food, estimates of energy expenditure can be derived from field measurements of water flux (Gettinger, 1984b; Green & Eberhard, 1983; Sapsford & Mendelsohn, 1984; Withers et al., 1980). In this regard, the ratio of water turnover rate to daily energy expenditure (WTR/DEE) has heuristic value. Since WTR/DEE = 0.10 for E.g. namibensis, it follows that DEE = WTR/0.10 (Withers et al., 1980). Assuming the same WTR/DEE ratio for free-living moles as captive moles, field metabolic rate was calculated as field water turnover rate (ml day^{-1})/0.10 = 17.3KJ day^{-1}.

Estimates of daily energy expenditure for Namib moles obtained in this manner were considerably less than measurements on laboratory animals (25.84 KJ day^{-1}) which were not involved in such energy consuming occupations as searching for food, mates and predator avoidance. Such low field metabolic rates reflect energy conservation and perhaps torpor. Earlier studies (Chap. 5) have postulated employment of diurnal torpor by Namib moles in their natural habitat as a means of reducing energy expenditure in an environment where food availability is limited. The results of this present investigation support these previous conclusions. Torpor occurs in many small desert mammals and as with *E.g. namibensis* is in most cases, linked primarily to energy conservation (Koford, 1968; Lindstedt, 1980a; Mullen, 1971; MacMillen, 1983). Since a lowered rate of metabolism results in a reduction of water loss in respiration as well as in the excretion of metabolites, torpor also serves as an effective water conserving mechanism (Bradford, 1974; Buffenstein, 1984b).

In caution, the precision with which the relationship between water turnover and metabolisable energy can be established depends largely on the accuracy of water turnover measurements and on the predictability of the water and energy content of the ingested prey (Sapsford & Mendelsohn, 1983). It has been demonstrated that isotopically determined water flux in *E.g. namibensis* is subject to some error. Furthermore, energy and water content of the Namib mole's major prey resource, the dune termite (*Psammotermes allocercus silvestri*), may differ from that of mealworms (Redford & Dorea, 1984), resulting in a different WTR/DEE ratio to that obtained in the laboratory. Thus estimates of field energy expenditure in *E.g. namibensis* must remain purely tentative until other experimental techniques are applied. Procedures anticipated include employment of doubly labelled water ($D^{18}O$ or $^3HH^{18}O$) for more precise determination of metabolic rates in free-living E.g. namibensis. This technique, developed by Lifson, Gordon, Visscher and Nier (1949) has since been used frequently and successfully on vertebrates (see Nagy, 1987 for review).

CONCLUSIONS

Like most successful small desert mammals, E.g. namibensis is nocturnal and fossorial, thereby avoiding environmental extremes. However, while nocturnality may enable moles to avoid excess water expenditure on heat dissipation, it does not provide an escape from the usual surface conditions of water scarcity. Exploitation of an insect food resource with a high preformed water content does not, as Morton (1980) suggested, remove the physiological problem of water conservation. For E.g. namibensis to remain independent of free drinking water necessitates an efficient kidney function for excretion of large amounts of urea in small volumes of urine. Low rates of energy usage and employment of torpor, although viewed primarily as adaptations to unpredictable variability in food supply, are further effective in reducing overall water requirements.

CHAPTER 7

GENERAL SUMMARY AND CONCLUSIONS

Nevo (1979) described subterranean mammals as 'fossorial species that spend most of their lives in sealed burrows and come to the surface only incidentally'. The commitment of subterranean mammals to life underground is manifested in several convergent structural and functional adaptations which reflect the simplicity of the subterranean ecotype that is an essentially sealed system, microclimatically stable, buffered against predation and low in productivity (Dubost, 1968; Ellerman, 1956; McNab, 1966; Nevo, 1979).

In this section, I will compare and contrast adaptive strategies of *E.g. namibensis*, an inhabitant of an arid sand dune environment, with those of other subterranean mammals, and identify the selective forces operating in this unique desert habitat.

Ecological Strategies

Subterranean mammals rely largely on below ground food resources, and since soil is a relatively dense medium, foraging in it is energetically very costly (Vleck, 1979, 1981). Not surprisingly, mechanisms that increase foraging efficiency are under relatively intense pressure. In herbivorous forms, behavioural adaptations to reduce burrowing costs include co-operative searching (Bennett & Jarvis, 1988; Jarvis, 1988) and adaptive burrow geometry (Anderson, 1982; Reichman, Whitam & Ruffner, 1982). For the Talpidae, which are carnivorous and their prey mobile, searching existing tunnels for food items is often more economically viable than searching for food by excavating undisturbed soil (Jensen, 1986).

Problems relating to foraging economics in E.g. namibensis differ from those of other subterranean mammals since construction of permanent underground tunnel systems in soft shifting sand dunes is impossible. Furthermore, productivity (plant and animal) is extremely low in the Namib dunes in comparison to other terrestrial ecosystems (Seely & Louw, 1980). To overcome these limitations, Namib moles employ an unusual surface foraging behaviour that reduces the costly search for food in an energy sparse environment. Although capable of taking a wide spectrum of animal prey, they opportunistically feed on termites, a clumped non-vagile prey resource generally found in association with sparsely distributed clumps of dune vegetation. For moles, the largest expenditure of energy is in locating patches of high resource availability, i.e. plants. Foraging efficiency is enhanced by non-random search patterns which are effective in encountering patches, and by employment of low cost surface locomotion when travelling between patches. Once an area of high prey availability is located, only then do moles switch to area intensive searching, using the far more energetically expensive but more effective prey locating sandswimming behaviour.

Surface foraging, although atypical for subterranean mammals, is not unique to the Namib mole, and occurs in the insectivorous marsupial mole (Notoryctes typhlops) (Howe, 1975) which, in Australia, inhabits a sand dune environment similar to that of E. g. namibensis. The giant golden mole (Chrysospalax trevelyani) is also a surface forager, but in a forest habitat (Maddock & Hickman, 1985). Since the energy cost of burrowing increases with body size, larger subterranean mammals have lower foraging efficiencies than small ones (Vleck, 1981). Presumably, the cost of foraging below ground for the largest of all insectivore moles, is prohibitive, particularly in a habitat where digging is further inhibited by dense roots systems.

Habitat productivity not only influences foraging behaviour, but together with an animal's energetic requirements (largely determined by body size) and diet, is an important determinant of home range size (Mall, Harvey & Clutton Brock, 1983). Herbivorous home ranges are significantly smaller than those of insectivorous subterranean mammals of similar size, reflecting differences in food abundance for the two trophic modalities as well as generally higher energy demands in carnivorous species (Kuyyper, 1979; Nevo, 1979). In spite of small size coupled with low energy requirements, E.g. namibensis has the largest home range area yet recorded for a subterranean insectivore, a reflection of the low food availablity in the Namib dune environment.

Nomadic home range utilisation by E.g. namibensis primarily reflects foraging considerations. Because of sparse and widely distributed food resources, Namib moles must travel extensively (up to 600m in a night) to meet their energy requirements. Rather than continual return to a central nest site or burrow, moles use temporary rest sites (usually situated beneath vegetation clumps) and forage in a different area of their home range each day. Many days may elapse before animals return to areas previously foraged, perhaps to prevent over exploitation of insect food resources.

Like all insectivorous and most herbivorous moles, E.g. namibensis is solitary and exhibits a strong home range fidelity. Since construction and maintenance of burrow systems requires considerable energetic investment, home ranges of subterranean mammals are generally also their exclusive and defended territories (Giger, 1973). In E.g. namibensis however, large home range size precludes effective energy efficient exclusion of intruders. Instead, a system of mutual avoidance and spatial time sharing appears effective in limiting encounters with neighbouring conspecifics.

Little information on the reproductive biology of E.g. namibensis was obtained during this study. Small litter size (Holm, 1969) and indications of a limited breeding season point to low recruitment rates. Longevity is not known for any golden mole (Hickman in press) but may be high in E.g. namibensis, since animals captured as adults survived three years in captivity. These findings suggest that Namib moles, like other subterranean mammals are 'k' selected, i.e. equilibrium species that are at or near the carrying capacity of the environment. Convergent 'k' selection in subterranean mammals reflects the stability and predictability of the subterranean ecotype (Nevo, 1979). Although the Namib Desert is characterised by short term variability (for instance, unpredictable rainfall resulting in irregular pulses of primary production), Seely and Louw (1980) have emphasised the long term stability of the dune environment, whereby accumulations of plant detritus form a continuous source of energy for primary invertebrate consumers such as termites. Thus population levels in Namib moles are maintained at low but stable levels, a response to a steady but limited food resource.

Physiological Adaptive Strategies

Physiological adaptations of desert animals centre mainly around the management of an efficient and economic water balance and a tolerable energy budget under conditions of high ambient temperatures and scarcity of food and water. Physiological adaptation, however, cannot be considered separately from behavioural adaptation. Behavioural adaptation complements and strengthens physiological adaptability and in a way compensates for the inaptitude of an animal's physiology by shielding it against climatic hardship.

Most subterranean mammals rarely leave their burrow systems and are thus subject to relatively constant temperature and humidity (Dubost, 1966; Kennerly, 1964), and continual darkness. Under these conditions of minimal environmental fluctuation, activity phasing in subterranean mammals is governed primarily by metabolic demands resulting in a characteristic polyphasic pattern. This is true even for arid dwelling species such as the pocket gopher (*Thomomys bottae*) (Gettinger, 1984) and the mole rat (*Spalax ehrenbergi*) (Nevo *et al*., 1982), where burrow systems provide protection against thermal extremes and desiccating conditions. In contrast, the Namib mole, as a surface forager, is potentially subject to rigorous diurnal conditions. Thus nocturnality in *E*.*g*. *namibensis*, as in many other small desert adapted mammals (MacMillen, 1972; Morton, 1982), is primarily associated with avoidance of high temperatures and the need to conserve water, but may also involve being active at a time when prey availability is most abundant, since most Namib dune invertebrates occupy this temporal niche (Robinson & Seely, 1980). In the case of *C*. *trevelyani*, the only other golden mole adapted to surface activity, predator avoidance as well as thermoregulation are implicated in nocturnal behaviour (Maddock & Hickman, 1985).

Activity rhythms of *E*.*g*. *namibensis* are endogenous and synchronised with the periodicity of the external environment by certain environmental cues. Entrainment of daily activity in Namib moles is apparently caused by the periodicity of rapid changes in light intensity, i.e. dawn and dusk experienced during surface foraging activities, while temperature appears to modify the timing effect of light on the initiation of activity. However, for the majority of subterranean mammals, conditions of constant darkness in burrow systems have resulted in the absence of a diel cycle governed by light (Hickman, 1984b; Vaughan & Hansen, 1961).

Physiological characteristics of E.g. namibensis shared with other chrysochlorids include low and labile body temperature, high thermal conductance and low metabolic rate. Withers (1978) maintained that poor thermoregulatory abilities of golden moles represent a physiologically 'primitive' condition. However, since similar energetic parameters are found in many other families of taxonomically diverse subterranean rodents, it is valid to consider such traits as adaptive and related to environmental factors (McNab, 1978).

The very low basal metabolic rate (22% of that expected on the basis of body mass) and extreme thermolability of E.g. namibensis greatly exaggerates the trend found in most subterranean mammals, including other chrysochlorids, but is consistent with the findings of Lovegrove (1986) in that aridity related factors are instrumental in selecting for lower metabolic rates in desert species. McNab (1966, 1979) suggested that because of a reduced potential for evaporative and convective cooling in warm humid burrows, prevention of thermal stress in arid zone subterranean rodents requires such a radical combination of small size, high thermal conductance and low metabolism that poor thermoregulatory abilities result, as exemplified by the naked mole rat, *Heterocephalus glaber* (McNab, 1966). However, in *E.g. namibensis*, avoidance of stressful temperatures can easily be achieved by behavioural means. Nocturnality allows escape from high air and surface temperatures when emerged on the dune surface, while during the day moles can burrow to depths where thermal conditions are moderate and stable. For these reasons, factors apart from thermal stress may also be important in selecting for the physiological traits of *E.g. namibensis*.

Firstly, when submerged in sand, the only air available to moles is limited to that in the pore spaces between sand grains. The very low metabolic rate of *E.g. namibensis* is thus viewed as a functional adaptation to reduce gaseous exchange in an oxygen poor environment.

Secondly, apart from the problem of breathing in sand, energetic considerations also play an important role in selecting for the unusual metabolic traits of *E.g. namibensis*. Vleck (1981) and Jarvis (1978) attributed the trend towards reduced metabolic and small body size in arid zone subterranean mammals as features needed to maintain low energy budgets in response to limited resource availability and the high energy expenditure concomitant with burrowing. Similarly in *E.g. namibensis*, the energetic parameters that govern precision in thermoregulation are linked to the minimisation of energy requirements in an environment where food resources are sparse. A low metabolic rate reduces energy expenditure and together with high thermal conductance and small size allows the use of low cost behavioural thermoregulation, whereby moles can gain or offload heat by simply moving to areas in the sand column which have a more favourable temperature. Should physiologically optimal sand temperatures not be accessible, as may happen during winter, moles employ daily torpor rather than indulge in the metabolically expensive process of maintaining thermal homeostasis by increased heat production.

It is of significance that none of the energy conserving features discussed above, i.e. reduced metabolic rates and torpor, have been described for any species of talpid mole (Jensen, 1983; McNab, 1979), and may be one of the factors limiting the distribution of this family to non-arid habitats.

In mammals, the turnover rates of energy and water are linked (Lifson & McClintock, 1966). Thus in Namib moles, low rates of energy usage and employment of torpor, although viewed primarily as adaptations to limited food resources, undoubtedly contribute to this species having one of the lowest water turnover rates recorded for a free-living insectivore. However, a low water turnover rate does not necessarily imply water independence which is essential for _E_._g_. _namibensis_ in its natural environment where free water is not readily available.

Eremitalpa _g_. _namibensis_ achieves water balance by utilisation of an insect food resource which has a high preformed water content, while nocturnality and burrowing habits preclude excess water expenditure on heat dissipation. Morton (1980) suggested that since moisture is a concomitant benefit of food intake in desert-adapted insectivorous mammals, there is no need for such species to expend any physiological effort conserving it. This argument does not hold true for E.g. namibensis which is able to reduce water loss by production of a concentrated urine, although this concentrating ability is moderate in comparison with that of arid zone granivorous rodents. Information on water metabolism in other subterrranean insectivores is completely lacking. Nevertheless, gross morphology of the kidney of E.g. namibensis indicates they are better adapted for water conservation than in the closely related, but mesic-dwelling, A. hottentotus.

To conclude, it appears that the physiology, ecology and behaviour of the Namib mole have all been influenced by the sand dune environment in which it lives, an environment which is arid, thermally demanding and energy sparse. An understanding of the foraging behaviour, home range utilisation and activity phasing of E.g. namibensis and the linking of these with their unusual physiology suggests that temperature, resource availability and a psammophilous habit must all be considered when seeking an explanation for the atypical features found in E.g. namibensis in comparison to those of other subterranean mammals.

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APPENDIX A

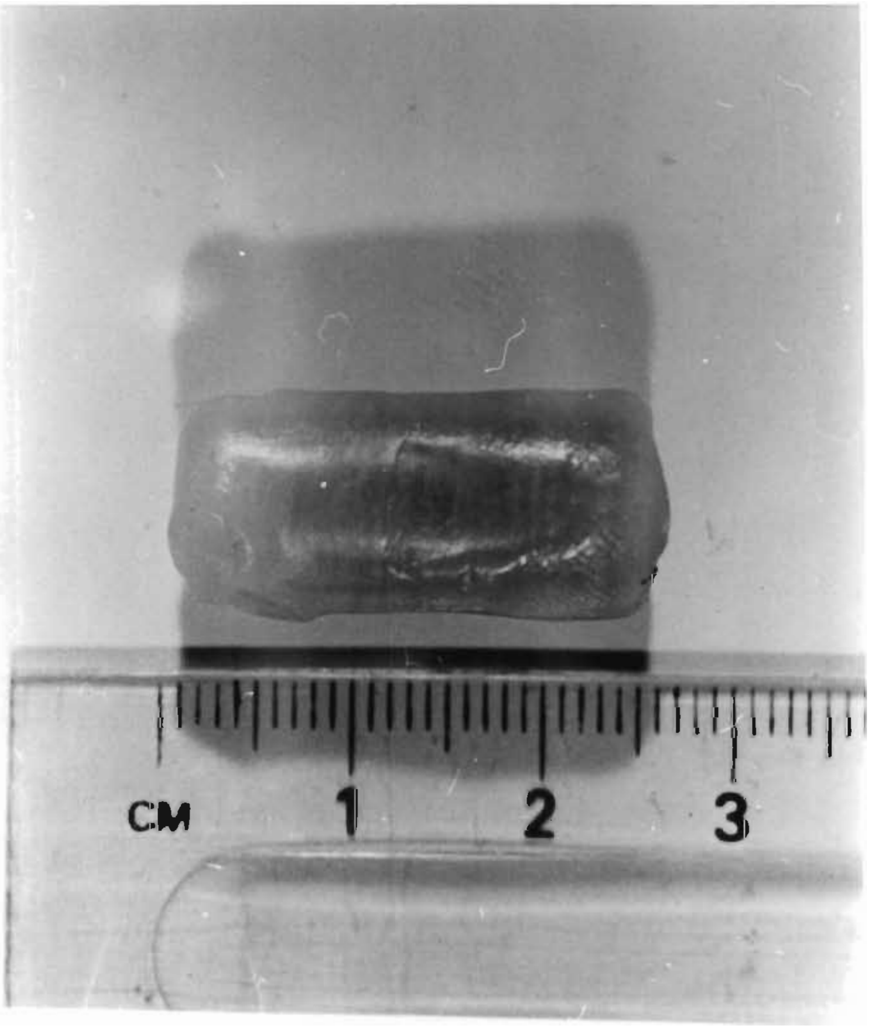
SURGICAL IMPLANTATION OF A TRANSMITTER PACKAGE IN A MALE EREMITALPA GRANTI NAMIBENSIS

A major problem in studying the ecology of E.g. namibensis has been the difficulty in locating individuals on consecutive days. In this appendix the feasibility of using implanted radio transmitters to locate free-ranging individuals is evaluated, with emphasis given to the effect of the implantation procedure on normal behaviour patterns. Internal implantation of transmitters was used instead of radio collars due to the fusiform shape of E.g. namibensis.

Surgery was performed under laboratory conditions using instruments sterilised with ethyl alcohol. A 25g male specimen was first anaesthetised with 15μl Saffan (Glaxovet) administered by intra-muscular injection into the shoulder. Induction time was five minutes, after which no movement occurred and the body was limp when handled. The mole was placed ventral side down in a sterilised dissecting tray, and a 1cm incision made with a sterile scalpel, longitudinal with the dorsal midline, just posterior to the shoulder region. Because of the loose skin in this region, stress on the sutures by the transmitter package was minimised with less chance of tearing.

The transmitter package was a sealed cylindrical unit, coated with paraffin-elvax wax, 2.2cm in length, 1.0cm in diameter and weighing 3.1g (Minimitter Model TM) (Plate A.1).

PLATE A.1: The small radio transmitter unit that was implanted in a male *E.g. namibensis*.


CM
1
2
3

Transmitter frequencies were in the 27-28MH$_2$ band, with a transmission range of 25-67m. The transmitter was inserted through the incision, aligned parallel to the dorsal midline (Fig. A.1) and the incision then closed with an absorbent gut suture material using four stitches.

Total duration from anaesthesia to completion of stitching was 20 minutes. After surgery, the mole was placed under a warm lamp in a terrarium (60 x 30 x 30cm) filled to a depth of 15cm with Namib dune sand to await recovery. Recovery time was 2.5 hours.

During ten days of post-operative observations, the mole continued to feed on mealworms (Tenebrio molitor larvae) supplied ad lib., maintaining a stable body mass, which seemed to indicate no serious harmful effects from surgical procedure. However, behaviour patterns deviated from normal with the mole usually remaining on the sand surface and appearing unbalanced during surface locomotion. Occasionally the animal would burrow, but only to very shallow depths with the dorsal aspect exposed. On day 11, the incision ruptured, exposing the transmitter, which was then removed surgically and the wound restitched. The mole recovered well and was released into the wild seven days later.

Overall, the technique was considered unsuccessful, since implantation of the transmitter greatly hindered normal behaviour patterns; nonetheless, the mole did recover well from surgical procedure. Use of a smaller transmitter package would likely have been more successful. However, no currently available transmitters appeared any better suited for the implantation procedure than the one used.