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

by

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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.

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

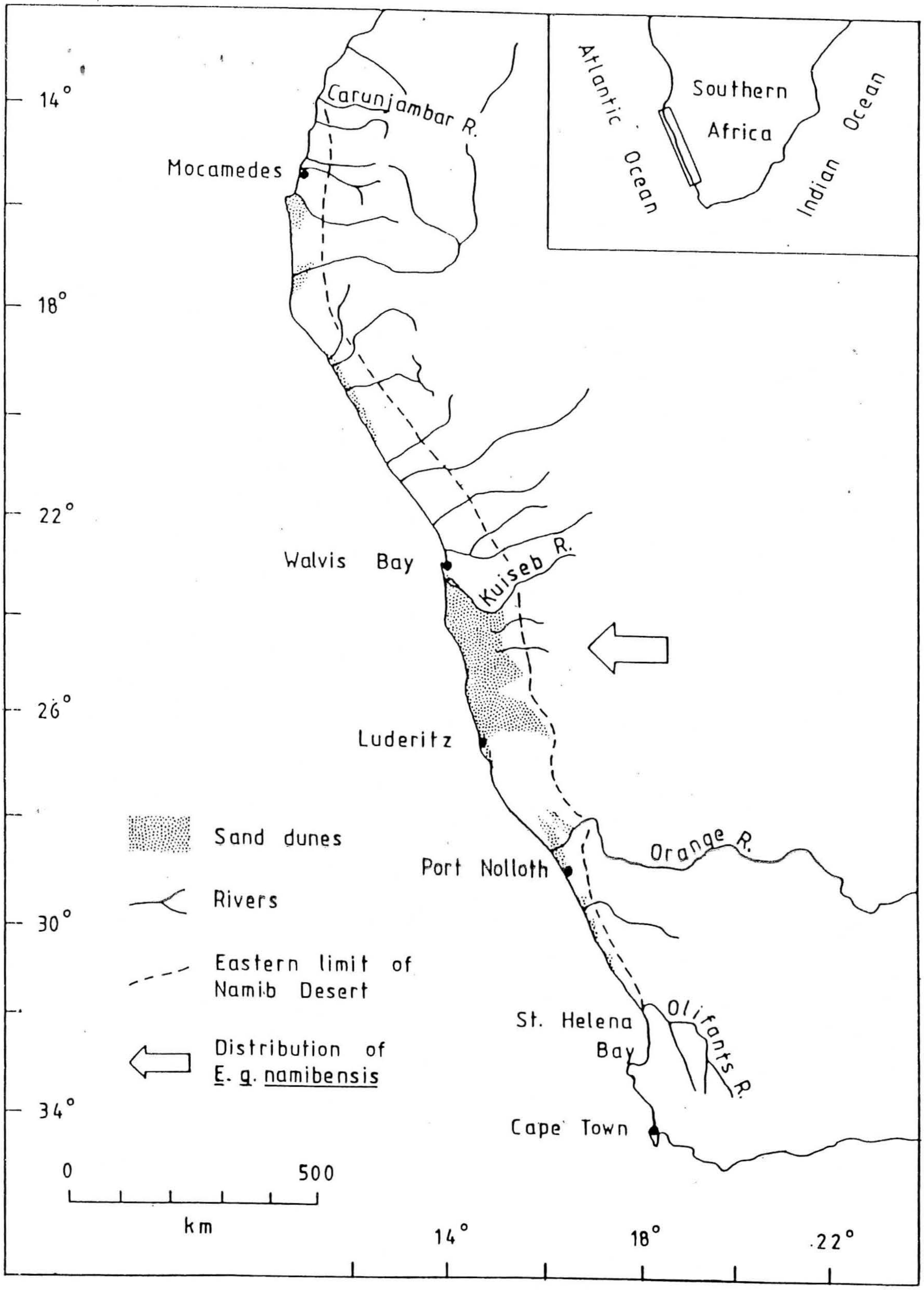

FIGURE 1.2: The Namib Desert with distributional range of E.g. namibensis indicated. Modified from Ward et al. (1983).

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^{o} 34'S, 15^{o} 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^{o} 45'S, 15^{o} 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.

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.

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 <u>E</u>. <u>g</u>. <u>namibensis</u> 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 (<u>Talpa</u> <u>europaea</u>) 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 0,01gm^{-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 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 (Eremitalpa granti namibensis) 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

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