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Feeding ecology and foraging behaviour of the Namib Desert golden mole, *Eremitalpa granti namibensis* (Chrysochloridae)

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(With 3 plates and 10 figures in the text)

Eremitalpa granti namibensis is a small, blind insectivorous mole endemic to the sand dunes of the Namib desert. Unlike most other subterranean mammals, *E. g. namibensis* lacks a permanent burrow system and forages for its prey on the dune surface at night. This study examines the natural dietary habits and foraging behaviour of *E. g. namibensis* in relation to resource abundance and distribution in the Namib dunes.

Stomach content analysis revealed termites as the major dietary item with other invertebrates being of only minor importance. Biomass of potential prey items was found to be low and food resources patchily distributed. It is suggested that desert moles opportunistically exploit a sedentary prey resource which occurs in patches of high concentrations, hence avoiding the energetic costs implicit in pursuing more mobile prey. Qualitative and quantitative descriptions of nocturnal foraging paths were undertaken so that searching behaviour could be related to the variation and distribution of food items. It is concluded that movement patterns of moles are effective in encountering localized areas of high prey concentrations and in minimizing energy expenditure in an energy-sparse environment.

Contents

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Introduction

The extensive underground burrow systems constructed by subterranean mammals provide 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 (Andersen, 1982; Jensen, 1986), especially in desert environments where productivity is extremely low (Louw & Seely, 1982).

The Namib golden mole *Eremitalpa granti namibensis* (Plate I) is a small (20–35 g), solitary, blind fossorial insectivore (Family Chrysochloridae), endemic to the dunes of the Namib Desert south of the Kuiseb River in Namibia (South West Africa). *E. g. namibensis* does not inhabit permanent burrow systems, but instead spends the daylight hours buried to depths of 5–35 cm 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 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 (Pyke, Pulliam & Charnov, 1977; Krebs, Houston & Charnov, 1981; Pyke, 1984).

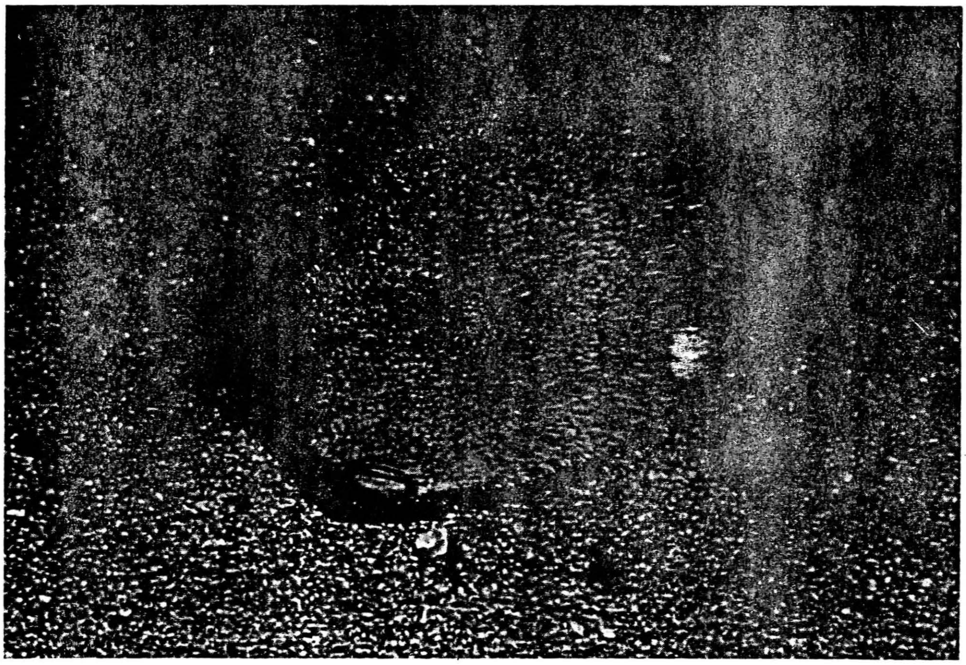

PLATE I. The Namib Desert golden mole (*Eremitalpa granti namibensis*).

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

1. Natural diet and food preferences.
2. Resource abundance and distribution in the natural habitat, the Namib dunes:
3. Qualitative and quantitative descriptions 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 2 study areas were located in the Namib dunes at Gobabeb (23° 34′ S, 15°30′ E) 58 km inland from the Atlantic ocean and at Far East (23° 45′ S, 15° 30′ E), 128 km inland from the Atlantic ocean at the eastern edge of the dune field. These 2 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, 3 from Far East) from December of 1983 to October of 1984. All moles were adults (9 males, 10 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 killed with chloroform. Stomach contents were prepared according to the methods of Funmilayo (1979) and Korschgen (1971). Stomachs were removed, put into 4% formalin for 24 h 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 (6 × 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. High frequency together with high volume indicates 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 & Poole, 1981).

Laboratory observations

Observations on feeding behaviour were made on captive animals maintained individually in (60 × 30 × 30 cm) glass terraria in the laboratory at 25 °C with a natural light cycle. Each animal was provided with Namib dune sand (10–15 cm depth) and a heat source in the form of a desk lamp equipped with a 50 W red light bulb in one corner of the terrarium. No feeding preference tests were conducted, but a large variety of different prey items were 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 3 dominant plant species, a woody dune succulent (*Trianthema hereroensis*), and 2 perennial grasses (*Stipagrostis sabulicola* and *Cladoraphia spinosa*).

Plants were selected at random and an area 0·25 m^2 was 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 0·15 m). Excavated sand was sieved using a mesh size of 0·04 cm^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 2–3 mm) was noted. Ten series of 60 samples (20 for each plant species) were taken at intervals of 1 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 fashion similar to that described above.

Animals extracted from samples by sieving were identified (to at least Order), counted and weighed. After drying to constant weight at 60 °C, items were reweighed and water content determined by subtraction of dry weight from wet weight. Weight of invertebrates was expressed as g dry weight 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. Weight of excavated invertebrates was again expressed as g dry weight 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 II). Tracks made by moles moving just below the sand surface are shown in Plate IIa. This behaviour, termed sandswimming by Coineau (1981) and Holm (1969), and described in considerable detail by Gasc, Jouffroy & 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 IIb). 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 IIc). The important feature of

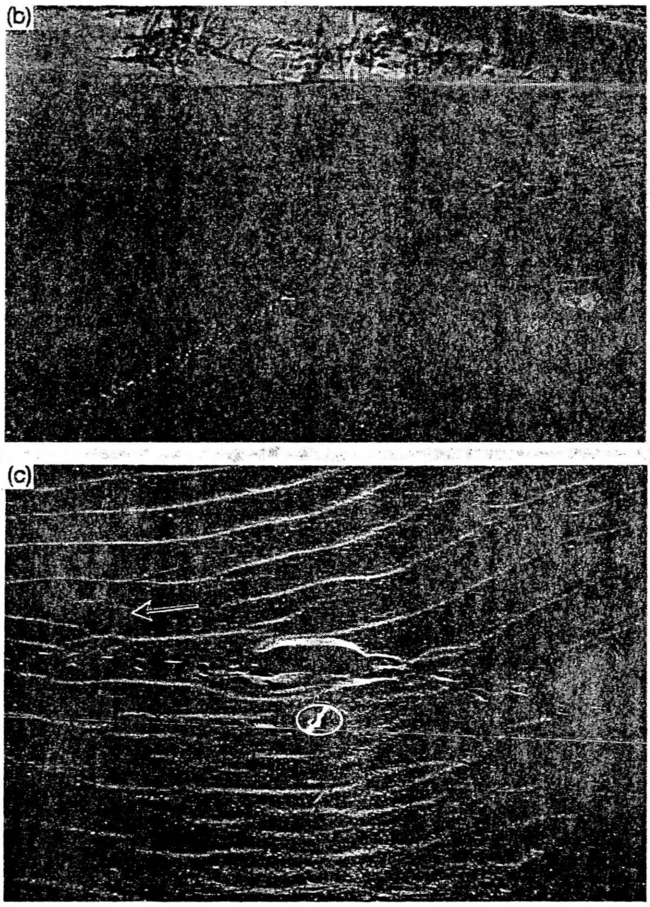

PLATE II. Tracks made by *E. g. namibensis* (a) Sandswimming. (b) Surface tracks. (c) 'Dip' on surface track. Arrow indicates direction of movement.

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. 1.

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

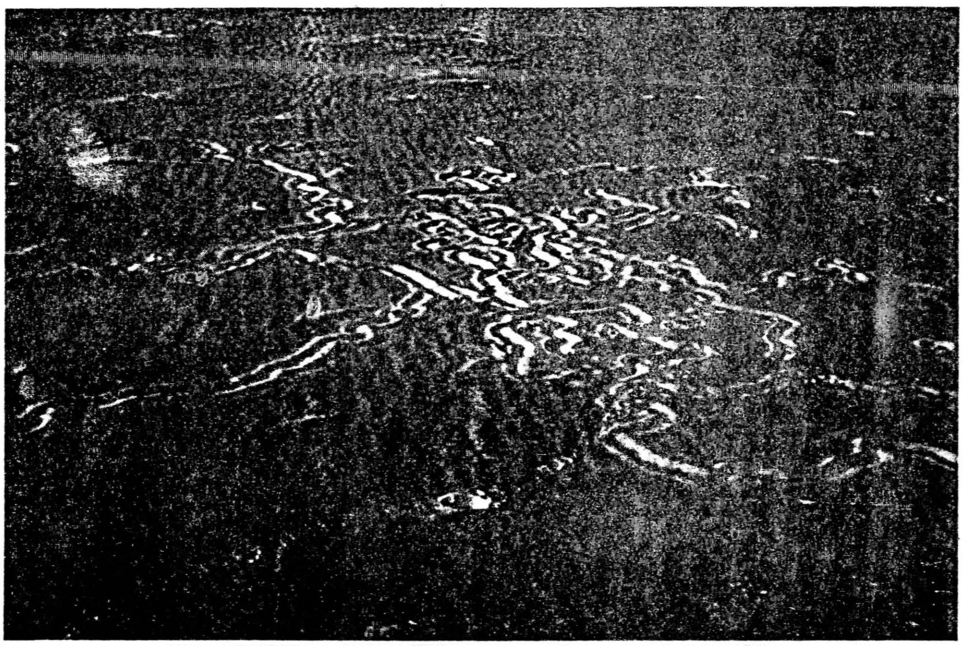

Plate III. Area concentrated searching.

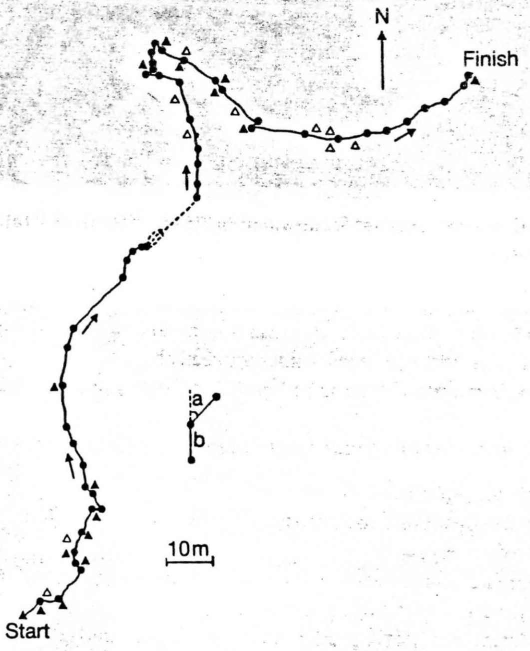

FIG. 1. Section of foraging path of *E. g. namibensis* mapped at Gobabeb. Solid (——) and broken (- - -) lines indicate surface and subsurface movement, respectively; solid circles (●) represent foraging dips; solid triangles (▲) are plants encountered along track; open triangles (△) are plants bypassed within 1 m of the track; a is angle of turn between successive moves, b is move distance between dips.

Results

Dietary composition

The three stomachs examined from the Far East area showed no marked differences in diet composition from those in the Gobabeb area. Thus Fig. 2 gives the percentage volume of prey items together with frequency of occurrence in the diet for the two areas combined.

Eremitalpa granti namibensis consume~~s~~d a wide variety of predominantly sand-dwelling invertebrates. Isopterans (*Psammotermes allocercus silvestri*) ~~are~~ were the major dietary item, both constituting the highest volume and occurring the most frequently. Coleopteran larvae ~~are~~ were the second most important food item. The remaining dietary components were included insect larvae, Araneida, Thysanura, Formicidae, Coleoptera and Skincidae, which are taken infrequently, with each contributing less than 5% of the total volume. Plant roots may have been incidentally ingested. All stomachs contained traces of sand as a consequence of prey being devoured below the sand surface.

Prey availability and natural food preferences

The relative availability of invertebrates obtained from dune slope and plant excavation at Gobabeb is presented in Fig. 3. The results are expressed as g dry weight m^{-2} since the weight 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, when tested by using the Kruskal-Wallis *H* test ($H=3{\cdot}92$; $P>0{\cdot}10$; $d.f.=2$). In comparison, the mass of invertebrates from the dune slope can be considered as negligible with a median biomass of zero.

The occurrence of termite workings ~~is~~ was also considerably greater under plants than on the dune slope. No significant differences in cast abundance were found between the three plant species

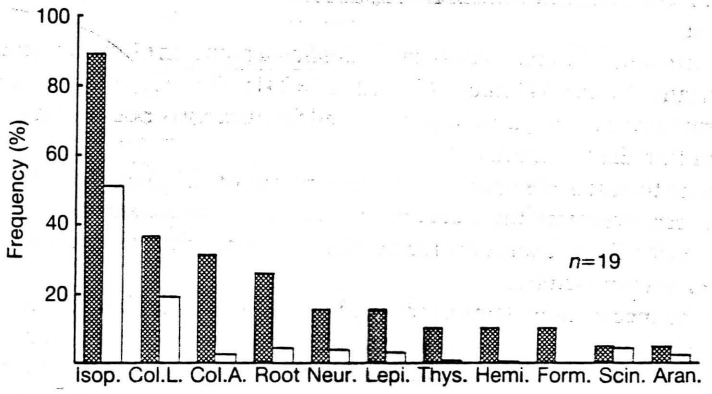

FIG. 2. Dietary composition of *E. g. namibensis* in the Namib dunes at Gobabeb and Far East. From left to right, abbreviations for Isoptera (Isop.), coleopteran larvae (Col. L.), coleopteran adults (Col. A), root material (Root), neuropteran larvae (Neur.), lepidopteran larvae (Lepi.), Thysanura (Thys.), Hemiptera (Hemi.), Formicidae (Form.), Scincidae (Scin.) and Aranidae (Aran.). □ % Volume; ■ % frequency.

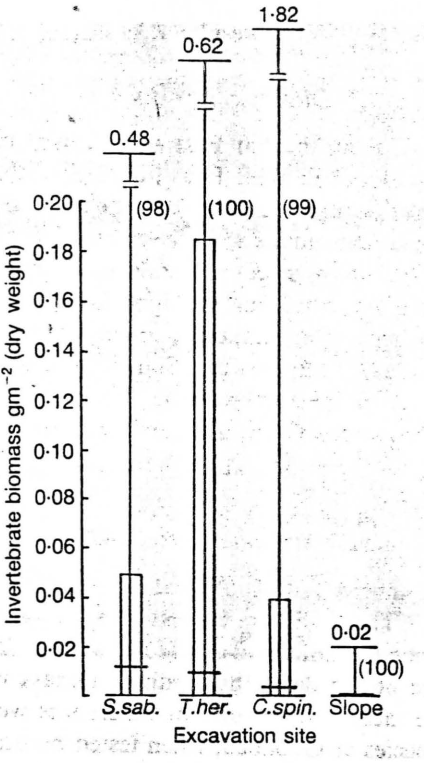

FIG. 3. Invertebrate biomass excavated from dune slope and dune plants (from left to right, *S. sabulicola*, *T. hereroensis*, *C. spinosa*) at Gobabeb. Horizontal bar indicates median value, boxes enclose lower and upper quartiles, vertical lines indicate range of values, numbers in parentheses give sample size.

($\chi^2=4{\cdot}1$; $d.f.=2$; $P>0{\cdot}05$), with the mean frequency of occurrence being 76% as opposed to 9% for the dune slope.

Differences in arthropod biomass between *S. sabulicola* plants in Gobabeb and Far East (Fig. 4) were not significant (Mann-Whitney *U* test: $U=241$; $P>0{\cdot}2$; $d.f.=20{\cdot}20$). Frequency of occurrence of termite casts in *S. sabulicola* compared favourably for both areas, being 85 and 75% for Gobabeb and Far East, respectively.

When attempting to assess the natural food preferences of *E. g. namibensis*, prey availability in the field ~~must be~~ was compared with the diet composition of the moles. Since only three animals were procured from the 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 is given in Table I. With regard to relative abundance of isopterans, coleopterans and thysanurans, there was is a marked contrast 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 comprised 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 probably reflects ed the small sample size of stomachs examined rather than their

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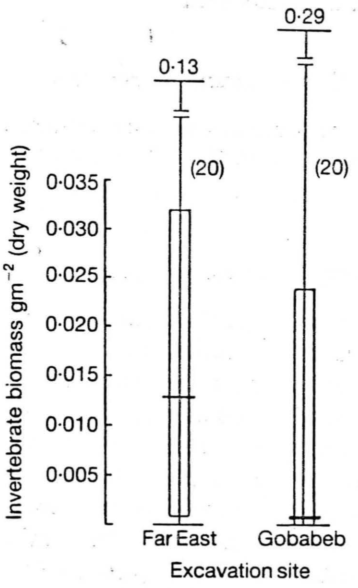

FIG. 4. Invertebrate biomass excavated from *S. sabulicola* at Gobabeb and Far East. Horizontal bar indicates median value, boxes enclose lower and upper quartiles, vertical lines indicate range of values, numbers in parentheses give sample size.

TABLE I

Dietary composition of ***E. g. namibensis*** *in comparison to prey availability at Gobabeb*

	Per cent 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
Aranidae	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
Solpugidae	0·0	0·2
Total items	2133	415

[a] Number of stomachs examined

[b] Number of excavation samples

rejection as a food source. No vertebrate taxa were collected from excavation samples, although lizards and snakes were present in the study area.

Water content of prey items

Mean percentage water content of some of the more numerous taxa of arthropods recovered from plant excavation ranged from 50% (S.D. ± 12; $n = 38$) for Coleoptera to 68% (S.D. ± 11; $n = 27$) for insect larvae.

Laboratory observation 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 meat.

The above items were placed on to 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. One 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 is shown in Fig. 5. There ~~are~~ were marked differences in path length between the two areas. Gobabeb tracks ~~may~~ extend ed to over 550 m in length, whereas at Far East 200 m was ~~is~~ the maximum, with most of the tracks measuring less than 50 m.

The proportions of surface to subsurface movement also differ ed between the two sites (Fig. 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 or 2 m at the beginning and/or end of the foraging track where the mole ha~~s~~d either submerged or emerged from its daytime refuge.
2. Around the base of plants.

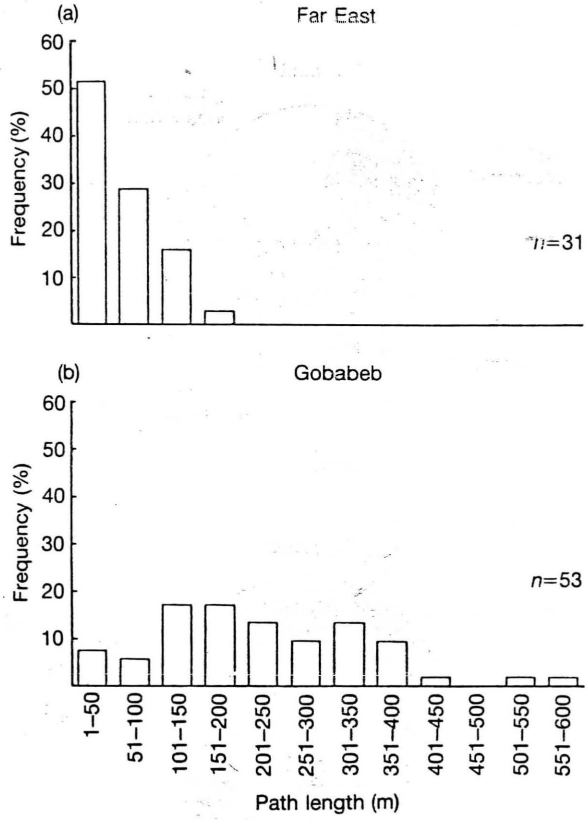

FIG. 5. Length of foraging paths of *E. g. namibensis* measured at Far East (a) and Gobabeb (b).

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 III).

At Far East, sandswimming was much more prevalent and not restricted to the three circumstances described above. In several instances the entire foraging path was subsurface. Area concentrated searching was not recorded at the Far East site.

Frequency distribution of the angles of turns between successive moves of mole tracks are shown in Fig. 7. Since these turns ~~have~~ had a circular distribution, it ~~is~~ 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. The Watson-Williams test was then used to test for differences between the mean angles of the two circular distributions.

Tracks from both areas showed a strong directional bias with $\bar{a}$ being 0° and 3° for Gobabeb and Far East, respectively. The mean angles for the two circular distributions were not significantly different ($F = 3{\cdot}84$; $P < 0{\cdot}05$; $d.f. = 1, 595$) although the angular deviation was greater for the Far East group of tracks. The proportion of left to right turns ~~is~~ was approximately equal and there ~~are~~ were few

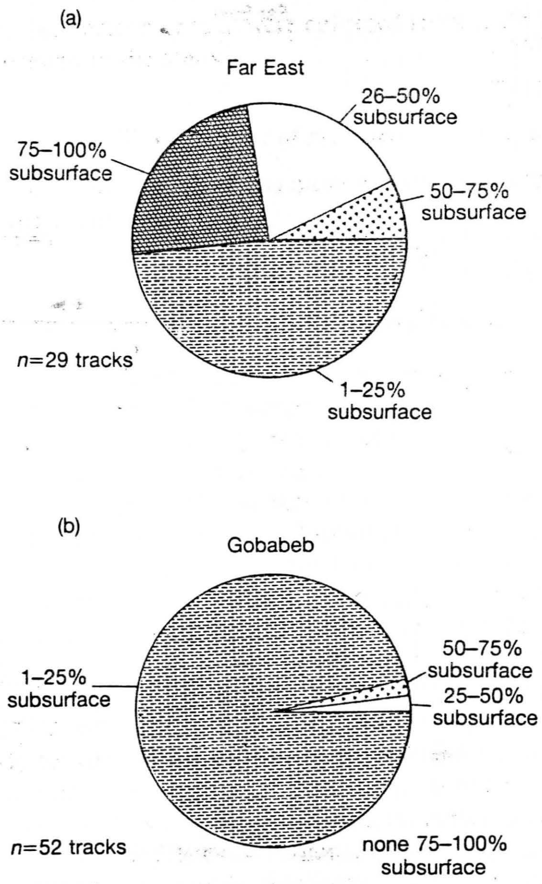

FIG. 6. Proportions of surface to subsurface movement for foraging paths of *E. g. namibensis* measured at Far East (a) and Gobabeb (b).

large angles of turn, illustrating clearly that foraging pathways seldom exhibit ed reversals of direction.

The frequency distributions for move lengths between dips (Fig. 8) show ed 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 II). Gobabeb tracks showed significantly more variation ($F = 1{\cdot}80$; $P > 0{\cdot}001$; $d.f. = 377,203$) than Far East tracks owing to the larger number of long moves, but no significant differences were found between mean move lengths when employing a Student's t test corrected for unequal variances ($t_s = 0{\cdot}287$; $P > 0{\cdot}05$; $d.f. = 580$).

The frequency histograms of move lengths (Fig. 8) and angles of turns (Fig. 7) fail to indicate whether moves or turns of given classes occur in random sequences or whether there are any regularities in the sequences. For example, do left and right turns tend to alternate or are short moves followed by short moves?

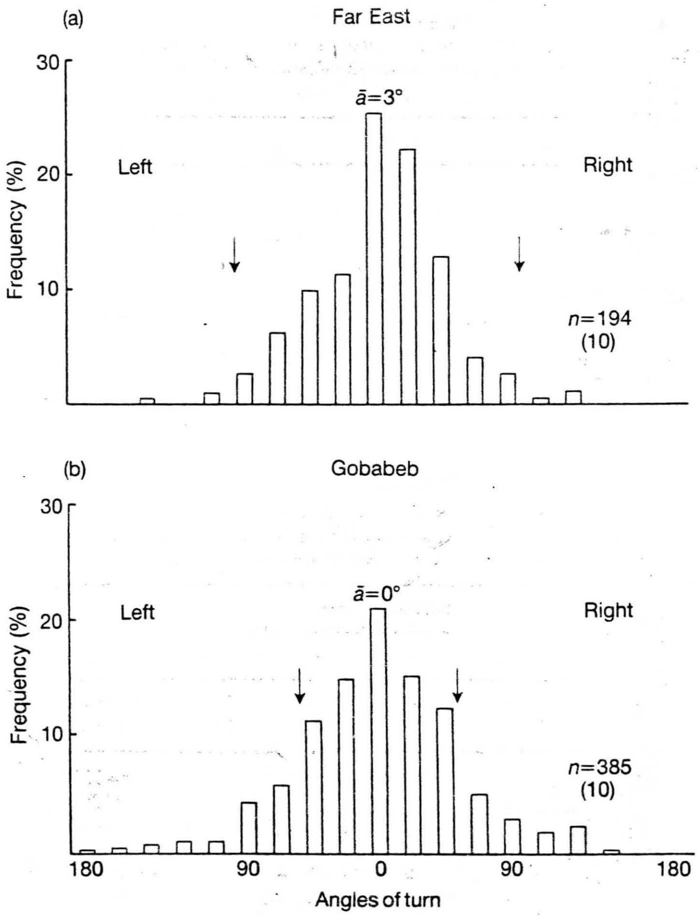

FIG. 7. Turn angles between successive moves of foraging tracks of *E. g. namibensis* measured at Far East (a) and Gobabeb (b). Numbers in parentheses indicate number of tracks measured, arrows enclose angular deviation. ā is the mean of the turn angles between successive moves.

Move and turn sequences were analysed according to the method of Smith (1974*a*). 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:

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

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

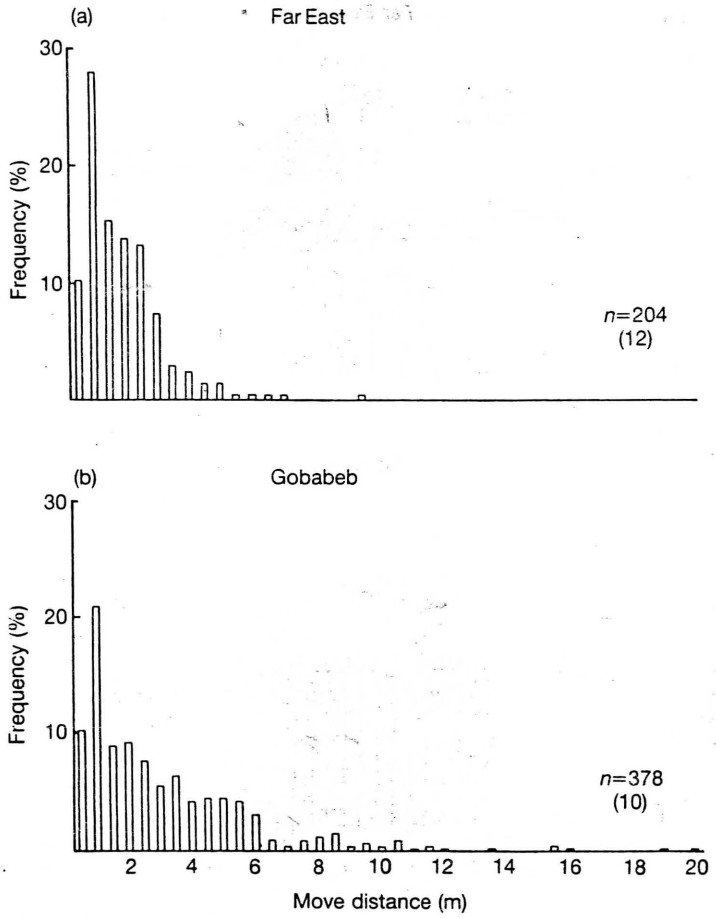

FIG. 8. Move lengths of foraging tracks of *E. g. namibensis* measured at Far East (a) and Gobabeb (b). Numbers in parentheses indicate number of tracks measured.

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 tests 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 χ^2 for sequences in each individual track were not possible because of unavoidably small sample sizes in many instances. Thus results of χ^2 testing (Table III) are based on the assumption that all tracks from one particular area were homogeneous in their turn and move sequences.

TABLE II

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		
$\bar{x}$	3·02	1·79
S	8·90	2·13
log $\bar{x}$	0·29	0·14
log S	0·18	0·10
Antilog (log x)	1·96	1·39
Antilog (log S)	1·50	1·25

TABLE III

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

		Move sequences					
Area	No. of tracks analysed	a	b	c	d	χ^2	P
Gobabeb	10	127	58	53	129	55·93	$<0·001$
Far East	12	58	38	38	56	6·81	$<0·01$

		Turn sequences					
Area	No. of tracks analysed	a	b	c	d	χ^2	P
Gobabeb	10	66	84	84	70	4·98	$<0·05$
Far East	12	16	41	36	85	3·36	$>0·05$

d.f. = 1 for all tests

The evidence from the chi-squared tests show that for tracks in both localities, there was a significant tendency for moves above and below the mean to occur in like pairs, i.e. moles tend to follow short with short and long with long moves. Referring to Fig. 1, it is apparent that the shorter moves take place when moles are foraging near plants or in areas of the dunes where termites occur, i.e. in association with 'area concentrated searching'. When the moles are travelling between plants or termite-rich localities, move lengths are increased.

Gobabeb tracks showed a clear alternation of left and right turns rather than like turns followed by like. The low χ^2 value for the Far East tracks indicated that turns happen in purely random sequences.

Figure 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 were tested for and found to be significantly different ($t=3$; $P<0·005$; $d.f.=37$) showing that the plant encounter rate at Far East is higher than that at Gobabeb.

The mean number of plants encountered per track at Gobabeb ($\bar{x}=19·11$; S.D. $=16·02$; $n=23$)

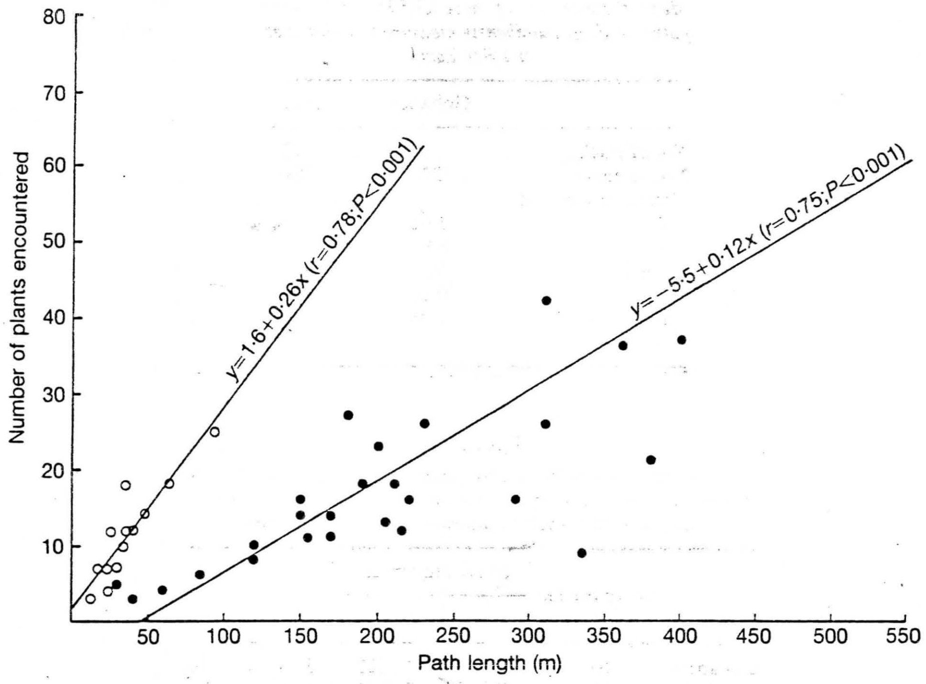

FIG. 9. Relationship between length of foraging track and number of plants encountered at Far East (○) and Gobabeb (●).

and Far East ($\bar{x}=11{\cdot}15$; S.D. $=6{\cdot}30$; $n=13$) did not differ significantly (t-test for samples with unequal variances; $t_s=0{\cdot}462$; $P<0{\cdot}05$; $d.f.=27{\cdot}12$).

The amount of subsurface movement around the base of plants encountered along the foraging tracks at Gobabeb is shown in Fig. 10. Relatively few plants had high foraging intensities, i.e. greater than 0·36 m of sandswimming movement.

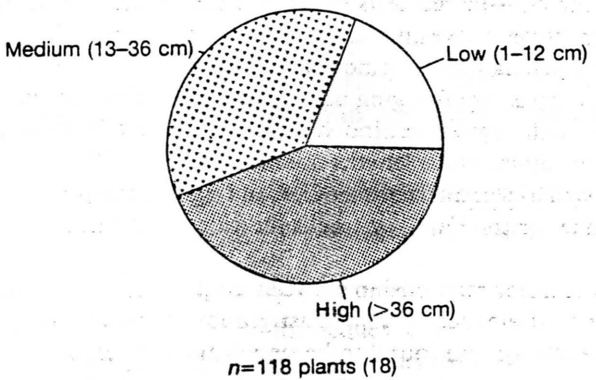

FIG. 10. Foraging intensity (amount of subsurface movement) around base of plants encountered along foraging paths of *E. g. namibensis* at Gobabeb. Number in parentheses indicates number of tracks on which observations were made.

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*, reports 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) record 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, specializing 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 (Schoener, 1969; Nevo, 1979), 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 desert moles is due to factors relating to the nutritional value and water content of these prey. Redford & 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 weight 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 & Dorea (1984) argue 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 (Skoczeń, 1966; Funmilayo, 1977).

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 (Perrin, 1980; Huey & Pianka, 1981).

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 & Weesner (1970) and Lee & 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 for other insect-eating vertebrates such as lizards (Robinson & Cunningham, 1978) attests 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 (Krishna & Weesner, 1970; Johnson & Whitford, 1975), 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, we believe 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 beetles and thysanurans. Similarly, as laboratory observations have shown, insect larvae, because of their sessile nature and soft body, are easier to catch and consume once detected 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 were predominant in the diets of *Cryptochloris 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 fossorial insectivores such as the European and North American talpid moles (Godfrey & Crowcroft, 1960; Raw, 1966; Rust, 1966; Whitaker, Maser & Pedersen, 1979) and is probably 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 (Lawrence, 1959; Koch, 1961; Seely, 1978; Robinson & Seely, 1980). However, no studies have specifically addressed the quantification of sand-dwelling arthropod fauna, although Seely & Louw (1980) have calculated a figure of 0·01 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 micro-environment and food (Seely, de Vos & Louw, 1977; Larmuth, 1979; Holm & Scholtz, 1980), are centres of termite activity and harbour both a greater number and a greater variety of organisms than do areas of open sand. Indeed, the biomass of invertebrates excavated from beneath vegetation clumps was a hundred times greater than 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 emphasize the patchiness of resource distribution.

Movement patterns of moles at Gobabeb

Differences in prey dispersion influence both foraging tactics and foraging pathways (Smith 1974*a*, *b*). 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 that will minimize 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 10 Gobabeb paths mapped 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) defines return time as 'time which elapses between successive visits to points'. Gill & Wolf (1977) have shown that in hummingbirds, timing of vists to flowers is a compromise between maximizing nectar accumulation and minimizing loss to other individuals. Similarly one would expect moles to utilize 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 because of difficulties experienced in following moles over long periods of time. The small amount of data obtained at Gobabeb does indicate that return time takes several days, since tracks monitored for three days did not return to the same patches.

The strongly onward-going nature of the foraging paths, together with the observation that plants are 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 fossorial insectivores (Eloff, 1951; Quilliam, 1966; Mellanby, 1971; Kuyper, 1985). The function of the foraging dip, although obviously important to prey detection, is not clearly understood. Laboratory observations indicate that vibrations resulting from prey moving in the sand can be detected by *E. g. namibensis* when it dips into the sand, while Van der Vyver Nolte (1968) report~~s~~ed 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 substratum 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 2 m from the base of plants (field observations), cannot be ignored.

Once a patch is encountered, the move lengths between dips are shortened, thus effectively keeping moles in patches after they have been located. Often, in such situations, moles will switch from surface movement to area concentrated sandswimming behaviour in response to high prey availabilities as for instance in areas of termite concentrations. Move lengths are longer between patches, so that the moles are travelling 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 to be effective when moles are emerged on the sand surface.

The number of patches encountered by an individual depends on the length of the foraging path. Laboratory studies (Fielden, *In prep.*) have shown that when food supply is restricted, moles exhibit 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 highlight 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

Eremitalpa granti namibensis is common prey of the owls *Bubo africanus* and *Tyto alba* (Nel, 1969; Skinner *et al.*, 1980; Tilson & Le Roux, 1983), and it is possible that the movement patterns described could easily be interpreted as avoidance of avian predators as is the case with foraging behaviour in desert rodents (Thompson, 1982; Kotler, 1984). The problem of whether a particular movement pattern is specifically adapted to the evolutionary goal of efficiency of 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 because patches were encountered at a higher rate, not because fewer patches were visited. Consequently, because moles need not travel so 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. Pyke (1984) has pointed out that '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'.

Summary

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 specialize 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 costs of foraging below ground for an animal the size of *C. trevelyani* must be prohibitive.

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