

Radioactive tagging has been used successfully to study the movements of subterranean insectivores in the field (Godfrey, 1955; 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 (Fielden, 1989). Also, the small detection range of radio isotopes 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 such as observing the construction of mole hills (Hickman & Brown, 1973) or the repair of flattened tunnelways (Hamilton, 1939; Arlton, 1936) has enabled the determination of periods of digging activity in fossorial mammals. This report demonstrates the usefulness of observations on surface tracks made by Namib moles (augmenting conventional capture, mark and recapture methods) as a technique for providing information on:

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

Materials and methods

Study area

The study site (59.50 ha) was situated in the Namib desert at Gobabeb (23° 34' S, 15° 30' E) on an eastward facing dune slope. This area was relatively homogeneous in biotic and physical characteristics and typical of the dune plinth zone (Robinson & Seely, 1980). The sparse vegetation was dominated by the dune endemic grasses *Stipagrostis sabulicola* and *Eragrostis spinosa*, and the dune succulent *Trianthema hereoensis*. These 3 species frequently formed large hummocks of 1–2 m high, where large accumulations of wind-blown detritus were found.

Location, tracking and capture of moles

The Namib mole is a surface forager, hunting mainly invertebrate prey on the dune surface at night while spending daylight hours buried 5–35 cm in soft dune sand. Mole tracks thus provide a clear record of an individual's movements on the dune surface during nocturnal foraging periods (Fielden, Perrin & Hickman, 1990).

A grid was used to monitor mole movements and population size. The grid had a cell size of 50 × 50 m (0.25 ha) and measured 26 × 9 cells.

Mole tracks present on the study grid were monitored on 2–5 days per month for an entire year. The number of separate tracks recorded on any one day on the grid was taken as representing the number of moles active during the preceding 24 h, since the dune surface was cleared daily by the natural effects of wind and sand movement. The delineation of all tracks encountered was plotted on to a scale map of the study grid. Sampling days were not always consecutive since inclement weather conditions of wind, and sometimes rain, could quickly obliterate tracks.

Moles were captured by digging them up out of the sand during the day, weighed, sexed and marked by toe-clipping prior to release at the point of capture. Capture success varied, with an average of 1 mole caught for every 5 tracks followed.

Captures and recaptures of marked individuals were each given a coordinate corresponding to 1 cell of the grid. In addition, grid coordinates were assigned to tracks if known to belong to a marked mole (confirmed by capture). Estimation of home range used the minimum area method (Southwood, 1978; Macdonald, Ball &

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Hough, 1980), where the centre point of all used cells for an individual were marked and a line drawn around these locations such that it enclosed the smallest convex polygon.

Results

Captures and numbers of moles in the population under observation

Population size in small mammals is usually estimated by the Peterson method or its derivatives (Caughley, 1977; Southwood, 1978), or alternatively a direct enumeration model using the minimum number of animals known to be alive (MNA) (Krebs, 1966). Such methods require that sampling be made at regular intervals and that the catchability of all members of the population is equal. These requirements could not be met in the present study since the efficiency of capture by hand was variable. Population estimates were made in two ways:

1. Mole abundance between July 1983 and July 1984 as estimated by the number of individual tracks counted on the study grid is shown in Fig. 1. The results indicate a fairly stable population size with an average of 9.68 ($n = 38$; S.D. ± 2.99) tracks counted per night.
2. The above estimate was supplemented by counting the number of individuals caught more than once (Reeve, 1982). Data on 16 captured moles are given in Table I. All were adults with the exception of one subadult female (No. 14). The number of recaptured animals indicates a population size of about 11 individuals during the study period, a figure close to the 9.7 derived from counts of tracks. A population density of between 0.17 to 0.19 moles ha^{-1} thus appears a reasonable estimate.

Home range size, stability and overlap

Home range area was measured for eight adults, all of which had been caught at least three times and for which a minimum of 11 grid locations had been obtained (Table I, Fig. 2). The size of the

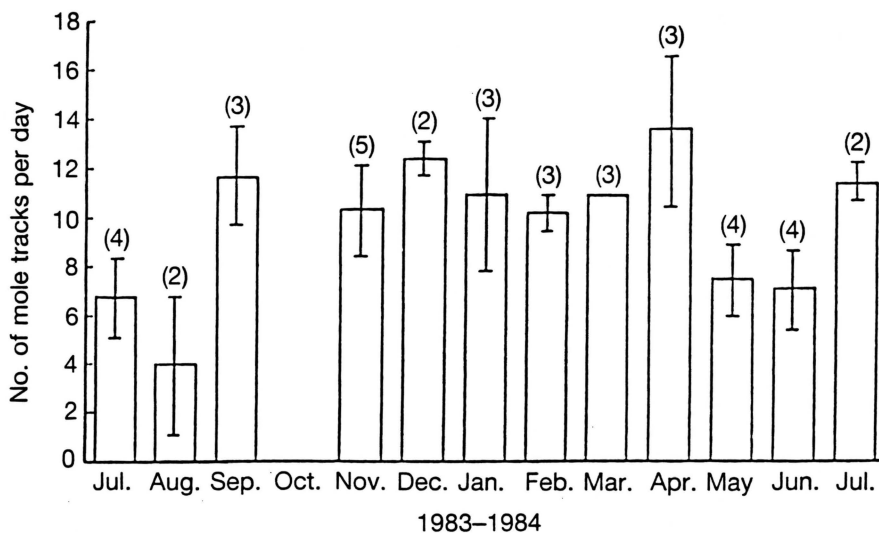


FIG. 1. Number of mole tracks on the study grid at Gobabeb. Columns represent mean values, lines indicate standard deviations, numbers in parentheses give number of days that tracks were counted. No data were collected for October.

TABLE I
 Captures, locations and home ranges of individual *E. g. namibensis* at Gobabeb

No.	Sex	Mass (g)	No. captures	Date of capture		Time ^a (days)	No. of locations ^b	H.R. ^c (ha)
				First	Last			
1	M	27	4	13.11.83	7.5.84	176	20	7.16
2	F	22	6	14.11.83	18.11.85	734	24	2.20
3	F	26	3	14.11.83	17.11.85	733	3	—
4	M	30	1	21.11.83	—	—	1	—
5	M	26	3	13.1.84	16.2.84	35	15	3.10
6	F	21	3	13.1.84	17.2.84	36	3	—
7	F	22	3	16.1.84	15.2.84	31	17	1.80
8	M	29	2	16.1.84	24.1.84	10	11	—
9	M	27	1	6.2.84	—	—	1	—
10	F	22	4	6.2.84	19.7.84	164	15	3.94
11	F	18	3	2.3.84	13.5.84	72	12	1.95
12	M	25	4	6.5.84	19.7.84	74	26	12.30
13	F	23	3	6.5.84	20.9.84	137	11	4.59
14	F	15	1	13.5.84	—	—	1	—
15	F	20	1	29.6.84	—	—	1	—
16	F	20	1	19.7.84	—	—	1	—

^a Time elapsed between first and last capture

^b Grid locations obtained from capture points and track positions

^c Home range

areas frequented by moles varied greatly. To ascertain whether this variability was significantly dependent upon the number of surveys carried out on each animal, the Spearman's rank correlation coefficient was calculated between the size of home ranges and the number of captures of each mole ($r=0.45$; $P>0.05$; $d.f.=6$), the number of grid locations for each mole ($r=0.45$; $P>0.05$; $d.f.=6$) and the number of days elapsed between first and last capture for each mole ($r=0.48$; $P>0.05$; $d.f.=6$). Since the results of these tests were not statistically significant, the importance of the above three variables was eliminated from the final demarcation of home range area.

Small sample size precluded reliable statistical verification of differences between male and female range size, thus mean home range area for eight adult moles of both sexes was calculated as 4.63 ha (S.D. ± 3.57). However, ranges of males (3.10–12.30 ha) were usually larger than those of females (1.80–4.59 ha).

Home ranges did show spatial overlay (Fig. 2), although the incidence and extent of temporal overlap was difficult to determine. Shaded portions indicate areas of overlap between animals which were known to be present on the study site within the same time period. For example, female No. 13 was recorded on the study site between May and October 1984 and thus overlapped in time with female No. 3 (November 1983–November 1984) and female No. 10 (February–July 1984), but not mole No. 5 (January–February 1984) (Fig. 2, Table I).

Moles tended to remain in the same general locality from year to year. For example, moles Nos. 2 and 3 (Table I) were relocated on a subsequent field trip to the study site in November 1985, within 100 m of their initial capture point two years previously.

Movement patterns and position of rest sites

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

A typical example of nightly movement patterns is shown in Fig. 3, which illustrates the position of surface tracks recorded on the study grid over three consecutive days. Tracks of 13 individuals were located on day 1 (Fig. 3a) (Nos. 1-13). On day 2 (Fig. 3b), 12 tracks were recorded including new paths for Nos. 2, 3, 4, 5, 7, 8, 9, 10, 11 and 13, and those of two animals Nos. 15 and 14 that had moved on to the study grid from peripheral areas. Movements of Nos. 1 and 12 were not monitored since they had moved off the grid on day one, while no fresh tracks were located for No. 6. On day 3 (Fig. 3c), four new moles moved on to the study grid (Nos. 16, 18, 19 and 20), while Nos. 2 and 8 moved off. No new tracks were detected for moles Nos. 5 and 7, but 3, 4, 9, 10, 11, 13,

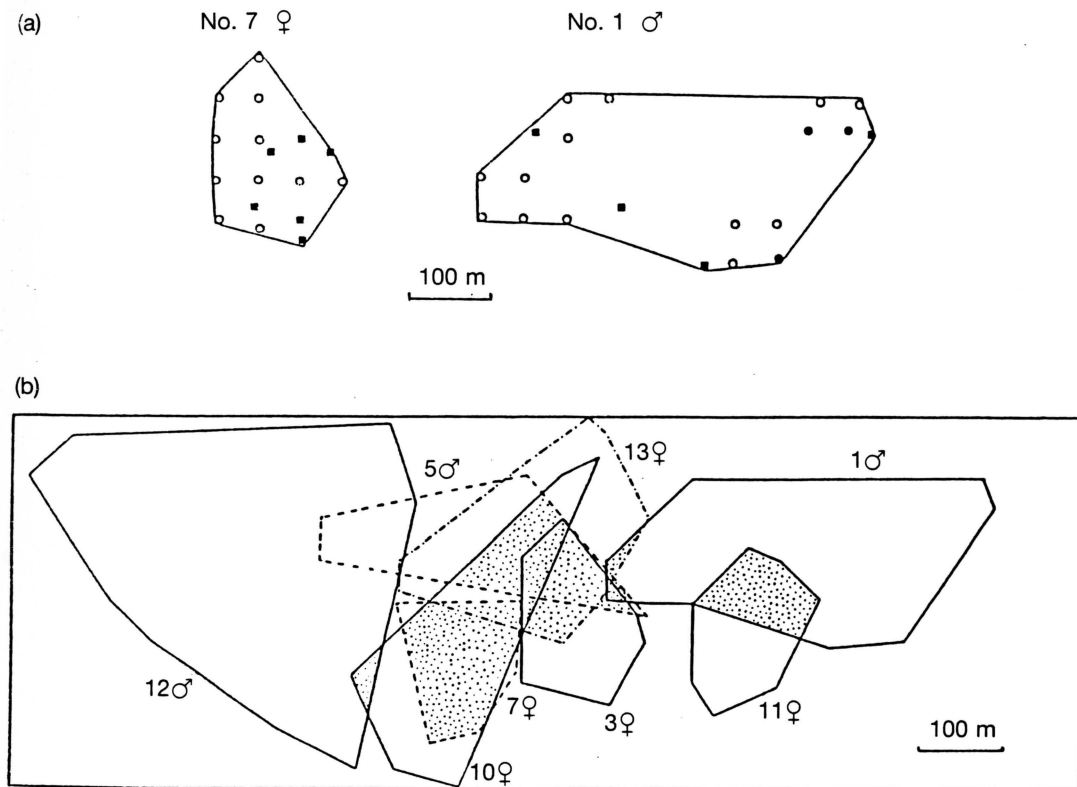


FIG. 2. (a) Example of home range estimation for two adult *E. g. namibensis* at Gobabeb. Solid squares (■) represent capture sites, solid circles (●) rest sites and open circles (○) track locations. Boundaries delineated by minimum area method. (b) Home ranges of eight adult *E. g. namibensis* measured between November 1983 and November 1985 at Gobabeb. Stippled portions indicate areas of temporal overlap between ranges, the rectangle delineates the perimeter of the study grid. See text p. 678 for further explanation.

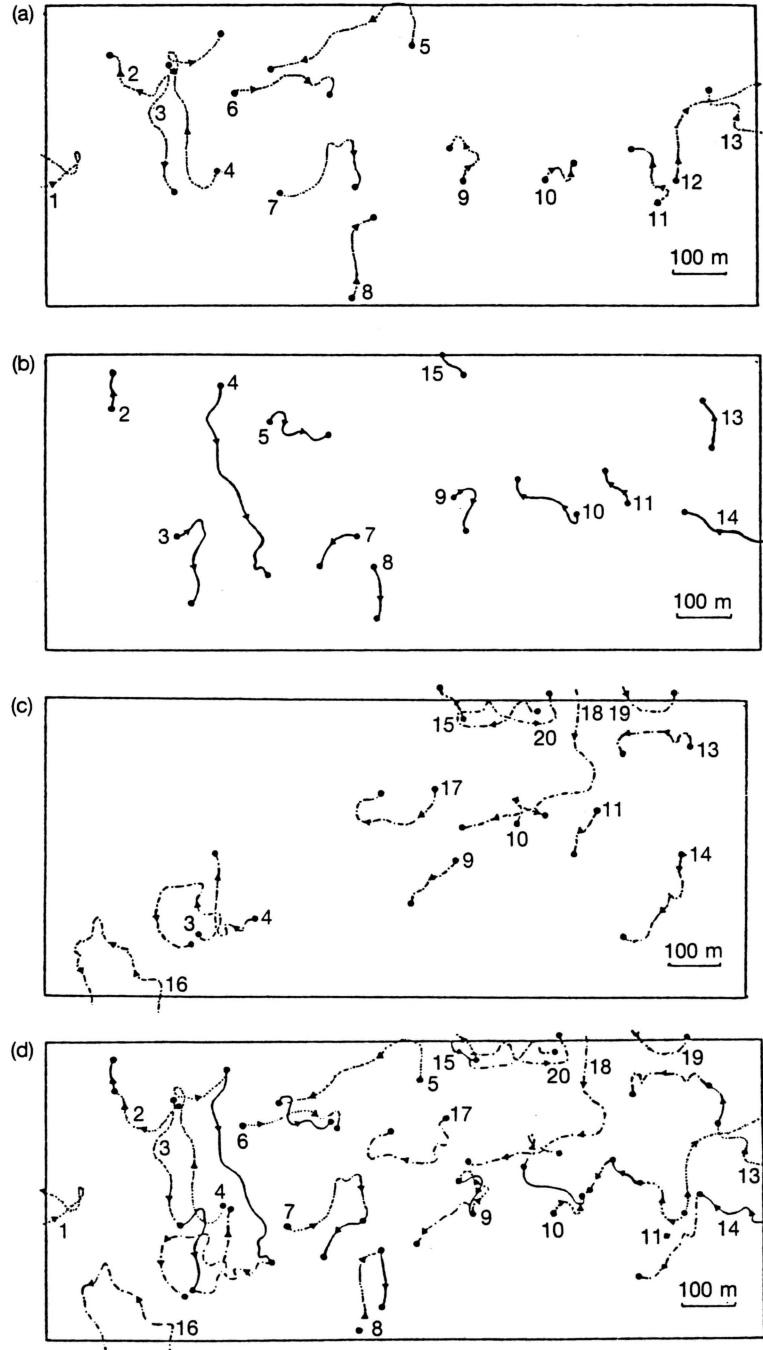


FIG. 3. Movement patterns of *E. g. namibensis* at Gobabeb over three consecutive days (a-c) with the cumulative record of three nights of activity shown in (d). Numbers refer to tracks made by different individuals, circles indicate rest sites and arrows direction of movement. The rectangle demarcates the perimeter of the study grid.

14 and 15 had all been active on the dune surface. A fresh set of tracks (No. 17) was found in the centre of the grid area, indicating that this individual had not been active on the surface for the two preceding days.

On any one night, foraging paths seldom traversed those of a neighbour. When track crossings did occur, there was rarely evidence of direct encounters between the two animals concerned, suggesting that such crossings were usually temporally separated. A cumulative record of three days of mole activity on the study grid showed clearly discrete centres of foraging activity between individuals (Fig. 3d).

Numerous excavations of rest sites (at least 100) never revealed any material or any form of permanent burrow or chamber. However, the situation of rest sites was clearly linked to that of vegetation coverage. For 88 recorded rest site positions, 81.9% were located beneath plants and only 18.1% in areas of unvegetated sand. Rest site sharing between two or more individuals was not observed, and instances of return to a previous rest site by the same individual were rare. Only three cases of rest site re-usage were recorded during the one year study period, which included 38 sampling days and 359 observations of tracks.

Discussion

Home range size and population density

Home range is the area used by an animal during its normal activities exclusive of excursions, migrations or emigrations (Burt, 1943; Jewell, 1966; Brown & Orians, 1970) and, intuitively, is 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, a primary determinant of home range size is likely to be access to, and distribution of, 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 affecting 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:

$$A = a \cdot W^b.$$

The value of the exponent b varies with the diet of the animals involved and on the type of statistical regression used (McNab, 1963; Harestad & Bunnell, 1979; Jenkins, 1981; Mace *et al.*, 1983; Lindstedt, Miller & Buskirk, 1986). However, as Lindstedt *et al.* (1986) cautioned, allometric equations are not precise predictive laws, but merely describe patterns. Thus 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. On the contrary, the mean estimate of home range size obtained for *E. g. namibensis* is far larger than those reported for other subterranean insectivores (Table II).

Primary and secondary production in the Namib dunes is among the lowest reported for any terrestrial ecosystem (Seely & Louw, 1980). Large home range size in Namib moles is thus believed to be essential for the acquisition of sufficient invertebrate prey to satisfy energy demands, in spite of these animals having a very low metabolic expenditure (Fielden *et al.*, 1990). Similarly, home ranges of other mammals inhabiting desert regions are typically larger than those of mesic-dwelling counterparts (Boulière, 1954; Petter, Lachiver & Chekir, 1984; Attuquayefio, Gorman & Wolton, 1986), probably because of the low productivity of desert environments (McNab, 1963).

TABLE II

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

Species	Body mass (g)	Home range (ha)		Reference
		Male	Female	
Chrysochloridae				
<i>Eremitalpa granti namibensis</i>	21	7.53 (3)	2.90 (5)	This study
<i>Amblysomus hottentotus</i>	66	0.02 (2)	—	Kuyper, 1979
Talpidae				
<i>Talpa europaea</i>	65–120 ^a	0.21 (1) 0.03 (3) 0.60 (1)	0.01 (1) 0.04 (10) 0.21 (3)	Godfrey, 1955 Haeck, 1969 Stone & Gorman, 1985
<i>Scalopus aquaticus</i>	50–170 ^a	1.09 (4)	0.28 (3)	Harvey, 1976
<i>Scapanus crarius</i>	50–170 ^a	0.15 (1)	—	Schaefer, 1982

^a Body mass range obtained from Walker (1968)

Species that inhabit low resource environments usually cannot maintain dense populations because of the limited 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 2–50 ha⁻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 foraged in different parts of their ranges each night and seldom returned to the same rest site occupied the previous day. 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 temperature (Fielden *et al.*, 1990).

Failure in this and other studies (Haacke, 1963; Holm, 1969) to find any form of permanent tunnel or nest chamber leaves the problem of breeding in *E. g. namibensis* unsolved. 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.

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 or 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*. The presence of such a chamber remains to be confirmed.

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 while van de Horst (1946) reported a seasonal breeding season (October–November) for the closely related *E. g. granti* collected from Port Nolloth, Namibia.

Movement patterns

The tendency for *E. g. namibensis* to utilize their home range in a circumscribed but nomadic fashion is believed primarily to reflect foraging considerations. Namib moles feed predominantly on non-vagile invertebrate prey such as termites and insect larvae (Fielden *et al.*, 1990). These food resources are sparse and patchily distributed and moles must travel considerable distances (up to 600 m a night) to fulfil their dietary needs (Fielden *et al.*, 1990). Rather than traverse the full extent of their ranges to return to a central nest site after each foraging foray, as do some species of desert rodents who store or consume food in their burrows (Schroder, 1979), it is more energetically expedient for moles to conserve energy by the use of temporary rest sites. In addition, it may be difficult for *E. g. namibensis*, being blind, to find its way back to the same resting site each night.

Moles must take several days to patrol their entire range since most tracks monitored for three consecutive days did not cover areas previously foraged. Fielden *et al.* (1990) suggested that moles utilize their home ranges in such a way that the return time to any particular area of the range has evolved as a balance between allowing food resources (emerging or reproducing insects) to renew and preventing loss to other moles.

Territoriality

Construction and maintenance of burrow systems by subterranean species entails considerable energetic investment (Vleck, 1981). Such species must invest more into areas they inhabit than do surface dwellers, and consequently may strongly resist displacement (Giger, 1973). Thus it is not surprising to find that home ranges of subterranean 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).

Namib moles are solitary and confine themselves to relatively constant home ranges to which they show fidelity, but not necessarily spatial exclusivity, as demonstrated by the varying degrees of range overlap between neighbours. Such overlap implies lack of territoriality, at least in the conventional sense of 'an exclusively defended area' (Burt, 1943; Brown & Orians, 1970). However, Kaufmann (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 Kaufmann, 1983 for review) in its explicit recognition of time as a territorial parameter, its rejection of exclusivity and overt defence 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 over three consecutive days showed discrete centres of activity for each individual with little evidence of any direct encounters with neighbours. Unfortunately, these observations were conducted on unidentified animals, thus the home range area for each was unknown, as well as the proportion of the home range utilized in the three day observation period. Nevertheless, the data are considered sufficient to demonstrate territoriality in *E. g. namibensis* as specified by Kaufmann'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.

This study suggests that Namib moles have overlapping home ranges which are too large for effective energy efficient exclusion of intruders. Instead, 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 (Kaufmann, 1983). Encounters with neighbouring animals may be reduced by some form of mutual avoidance behaviour, since in my limited observations no evidence of 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.

For a system of mutual avoidance to operate successfully, an individual must be able to recognize its immediate neighbours so that it can organize its routine activities and minimize contact with them. In the Pyrenean desman (*Galemys pyrenaicus*), range demarcation is affected by the continual renewal of scent marks from faecal and sebaceous sub-caudal glands (Stone, 1987), while in *Talpa europaea*, burrows are marked regularly by the inhabitant through micturition (Mellanby, 1966). Some form of scent-marking may occur in *E. g. namibensis*, possibly at rest sites lying beneath plant hummocks, since shifting sand does not provide a good substratum 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.

Summary

The population density of moles in the Namib desert appears low in comparison to that of other subterranean insectivores in non-arid environments. Furthermore, sparse and widely-dispersed food resources require moles to have large home ranges which they utilize in a nomadic fashion rather than continual return to a central nest area. Like other subterranean insectivores, Namib moles are solitary and appear to have a strong home range fidelity, although ranges of neighbouring animals do overlap. However, mutual avoidance, perhaps facilitated by scent, appears to play an important role in reducing the frequency of encounters between individuals in the natural situation.

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