

ACTIVITY PATTERNS IN THE MOLE-RATS *TACHYORYCTES SPLENDENS* AND *HELIOPHOBIUS ARGENTEOCINEREUS*

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ABSTRACT

Activity in two unrelated genera of mole-rats, *Tachyoryctes* and *Heliophobius*, was studied in the field by recording the movements of animals tagged with radioactive wire. *Tachyoryctes* shows a single marked activity peak and only leaves its nest between 10.00 and 19.00 hour. *Heliophobius* shows a more dispersed and prolonged activity pattern although peak activity occurs over approximately the same period as in *Tachyoryctes*. *Heliophobius* spends over 50% of the day out of its nest, *Tachyoryctes*, under 25%.

These differences can be attributed to a different function of the nest in the two genera (*Tachyoryctes* has a multipurpose nest; *Heliophobius* uses its nest solely for rest), and also to the fact that *Tachyoryctes* has light-sensitive eyes whereas *Heliophobius* appears unable to appreciate light; *Tachyoryctes* periodically comes to the surface to forage and this exposure to light may trigger the 24-hour activity cycle.

INTRODUCTION

The mole-rats *Tachyoryctes splendens* (Rüppell) and *Heliophobius argenteocinereus* (Peters) are strictly fossorial rodents, they live in burrow systems of their own making and rarely come above ground. Field observations of their activity are severely hampered by their fossorial existence. This indeed has, until recently, been a limiting factor in studies on activity in many fossorial mammals.

The development of radioactive tagging techniques has made it possible to study the activity of fossorial mammals in their burrows and under natural conditions. Godfrey (1955) labelled *Talpa* with Cobalt-60 tail rings and then followed their movement underground with a Geiger-Müller counter. Similar methods have been applied to mole-rats in this present study.

Tachyoryctes splendens (Family Rhizomyidae) is a solitary aggressive mole-rat. Adult males have an average weight of 250 g and females 218 g. However, considerable weight variation is found between adult animals. *Tachyoryctes* has a discontinuous distribution over much of East Africa, Ethiopia and eastern Congo (Misonne 1968). It is a ubiquitous feeder on a variety of grass and herb roots, stems and leaves. It uses its well-developed incisors to dig out a burrow system about 30 m long. A major portion of this system consists of foraging burrows which run at a depth of 15 to 25 cm. A deeper nest (30 to 60 cm) and a bolt-hole are also present. The nest chamber is a large multipurpose chamber in which sleeping, defaecation and food-storage take place. The burrow system and mode of burrowing are described in detail elsewhere (Jarvis and Sale 1971).

Heliophobius argenteocinereus (family Bathyergidae) is, like *Tachyoryctes*, solitary and aggressive. Sexual dimorphism is not apparent and adult animals weigh an average of 160 g. *Heliophobius* occurs over much of central and eastern Africa (de Graaff 1968). The foraging burrows run at similar depths to those of *Tachyoryctes* but the total length of the system is considerably greater (about 47 m). Unlike *Tachyoryctes*, food storage and defaecation are not associated with the nest chamber. The tubers on which these animals feed are not stored in a special chamber but instead, are left growing in the foraging burrows. The mole-rat visits an

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exposed tuber and eats a portion from it at each meal. Further details on burrowing and burrow systems are given elsewhere (Jarvis and Sale 1971).

A comparative study of the activity of these two mole-rats is of particular interest because they belong to families which are phylogenetically unrelated. The Rhizomyidae are Myomorph rodents, whereas the Bathyergidae are probably highly specialised Hystricomorphs. The many similarities between these two families can be attributed to convergent evolution in response to their fossorial mode of life.

METHODS

ACTIVITY IN *Tachyoryctes*

This was studied in the field and most observations were made at Chiromo Estate, Nairobi, Kenya. The study was in two parts:

(i) *Mound building activity*

Between mid-December 1968, and early July 1969, a weekly count was made of the mole-hills (mounds) thrown up on a 50 m² plot of ground.

In a near-by area were placed seven gypsum blocks of the type used in measurements of soil moisture. They were buried at depths of 15, 30, 61, 122, 156 and 183 cm. Weekly readings of the resistances of these blocks (giving the relative soil moisture) were taken with a "Sciex" moisture meter and the results were correlated with mound-building activity.

The study period was chosen as ideal to cover the full range of soil moisture conditions normally experienced by mole-rats. Thus, December to mid or late March should have been very dry and April to May very wet; with periods at the onset and end of the rains when the soil was moist. Unfortunately, the rains were unseasonal and the dry season broke prematurely in late January 1969. Thereafter, intermittent rainfall kept the soil moist and the normal heavy rainfall of April and May did not materialize. The rainfall figures for the study period were obtained from the Meteorological Department, Nairobi.

At the end of the study period all the mole-rats in the study area were caught. The population was found to consist of one adult and two sub-adult females. The latter occupied the same burrow system and were approximately three months old (from their weights). No sign of their mother was found. The adult female had occupied a system spatially distinct from the sub-adult animals throughout the study period.

(ii) *Activity of tagged Tachyoryctes*

Tantalum-182 wire was used in tagging three other mole-rats. It was chosen for its relatively short half-life (about 100 days) and because its high energy gamma-radiation could penetrate through a considerable thickness of soil.

Pieces of wire, about 5 mm long and with an approximate radioactivity of 0.5 mc, were encapsulated in plastic tubing (to protect the animals from β radiation) and inserted subcutaneously. Tail rings similar to those used by Godfrey (1955) were impracticable as the mole-rats would have speedily bitten off the rings.

The tagging procedure was as follows: Mole-rats were live-trapped, immediately anaesthetised with ether and a capsule inserted under the skin on the back via a 5 mm incision. Two stitches closed the wound at the site of insertion and the area was painted with gentian violet to prevent infection. When fully recovered from the effects of the anaesthetic (30 to 60 minutes) the mole-rat was released into its original burrow system. Once back in the burrow, the mole-rat appeared to act normally and would rapidly seal the opening in its burrow with soil.

Using a portable Geiger-Müller counter with earphones (Beta Probe Unit, type 1292A; connected to a Ratemeter, type 12921 Ericsson Telephone Ltd.), the ground surface of the area was then systematically searched until the animal was located, its movements could then be followed. In studying activity in these animals considerable time was saved by first locating the nest. Once known, this area was checked before a search was made of other parts of the system. Animals could be detected to depths of about 60 cm below ground.

It was practically impossible to follow a moving mole-rat. Movements were too rapid and the possible routes taken too numerous to permit continuous monitoring. With practice, however, it was possible to rapidly relocate the animal once movements ceased; this was particularly true after an animal had been followed for several days and some idea of the plan of the system and the areas favoured by the mole-rat had been gained.

A device for automatically recording movements in and out of the nest area was used on two *Tachyoryctes*. A radiation alarm similar to that described by Inglis, Post, Lahser and Gibson (1968) was placed above the nest and attached to a small geiger counter (Panax Monitor Type TM 64G), and these in turn coupled to a Leeds and Northrop Speedomax "H" recorder. When the pulsed output from the geiger counter rose above the specified threshold (to discriminate against background radiation), a relay was activated and a recording was obtained. With this, movements of the tagged mole-rats in relation to the nest could be automatically recorded. The circuit for the radiation alarm component differed slightly from that of Inglis *et al.* (1968) and is given in Figure 1. The daily activity rhythms (in and out of the nest) of one adult female and one adult male *Tachyoryctes* (mole-rats B and C) were obtained by this method. One other animal, an adult female (mole-rat A), was also tagged and used in a more detailed study of daily activity. A brief case history of the tagged mole-rats follows:

Mole-rat A

Adult female: weight when tagged=315 g

Date tagged: 12 August 1968

Lost tag: 29 August 1968

Recaptured: 3 September 1968

Weight on recapture=300 g.

Comments: The mole-rat appeared in excellent health on recapture. The tag had worked its way out through the skin and was later recovered in a faecal pellet in the nest chamber. The wound was well healed. The mole-rat was kept under observation in captivity and was still healthy 10 months later (July 1969), but the fur at the old tag site had turned white. Mole-rat A was used for a detailed study of daily activity (see Figures 6 and 7).

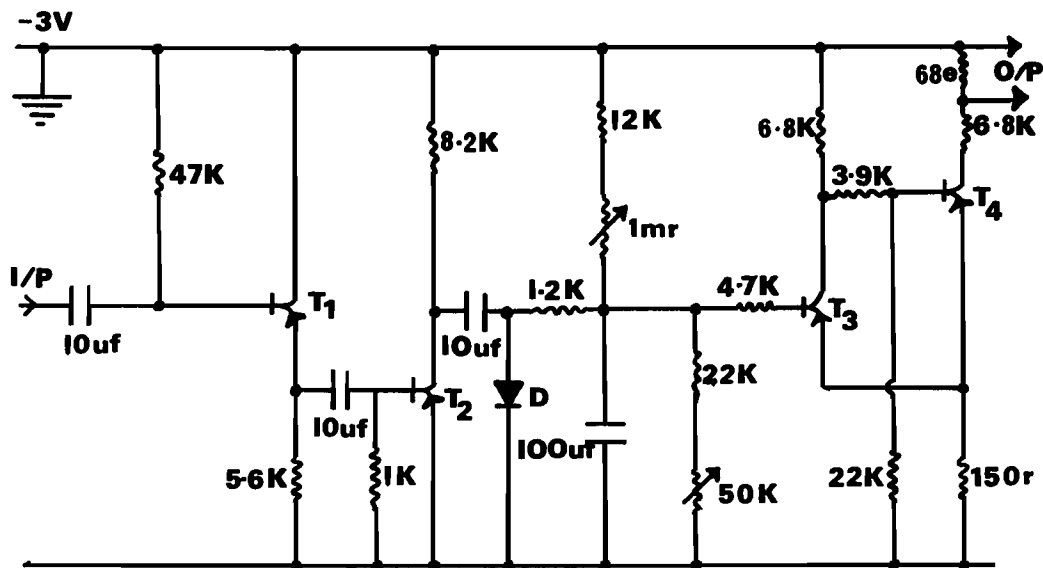


FIGURE 1

The circuit for the "radiation alarm". Modified from Inglis *et al.* 1968 (T_1 , T_2 , T_3 and T_4 = OC 71; D = OA 85).

Mole-rat B

Adult female (lactating): weight when tagged = 196 g

Date tagged: 9 October 1968

Recordings began: 17 October 1968

Recordings ended: 13 November 1968 (tag lost).

Comments: All attempts at recapture were unsuccessful. The mole-rat was active (new mole-hills thrown up) but was extremely trap-shy and detected and plugged all traps set in her system. Her tag was recovered in one of the foraging burrows. Details of the activity of mole-rat B are given in Figure 3.

Mole-rat C

Adult male: weight when tagged = 260 g

Date tagged: 1 February 1969

Recordings began: 8 February 1969

Recordings ended: 12 April 1969.

Comments: The mole-rat was recaptured on 12 April because the recordings showed a marked decrease in daily activity. The animal was found to be very thin and weak. Its weight on recapture was 175 g and it had an area of necrosis at the site of the tag which appeared to cause the animal much discomfort. The tag was removed and the animal kept under observation; it rapidly

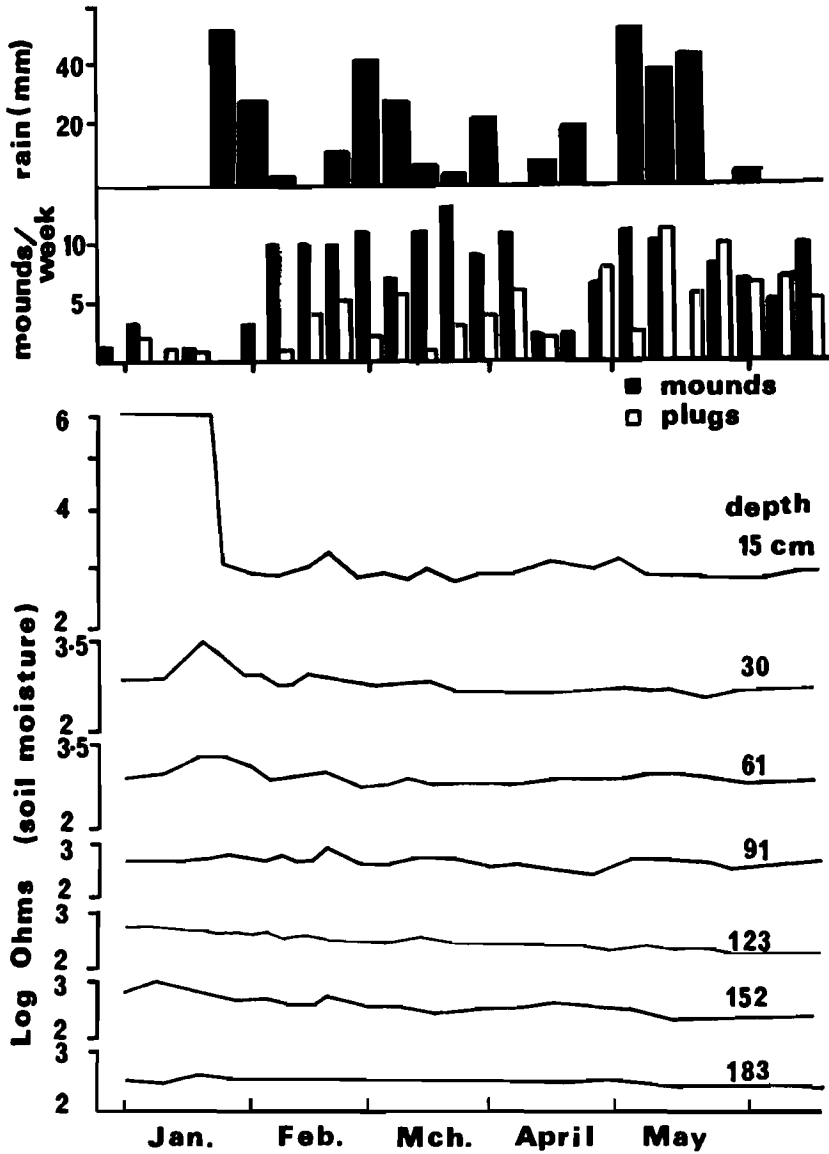


FIGURE 2

To show the rainfall, soil moisture and weekly total number of earth plugs and mounds produced by *Tachyoryctes* in a 50 m² plot of ground.

Relative soil moisture is shown by readings (in log ohms) of the resistances of gypsum blocks buried at different depths. The higher the reading, the lower the soil moisture content.

recovered its original weight and the area of necrosis healed but lacked fur. The animal was killed on 21 May 1969, and the autopsy showed no sign of radiation damage. Portions of the liver, small intestine and testis were sectioned and on examination by light microscopy appeared normal. The suggested cause of loss of condition was the area of necrosis which made digging and foraging activities painful. Details of the activity of mole-rat C (excluding April) are given in Figure 4.

The gap between the date of tagging mole-rats B and C and the beginning of recording was largely due to difficulties in locating the nest. The burrow systems were well established and the mole-hills old and no longer obvious, consequently the limits and direction of the burrows were unknown. A wide potential area of tall grassland had therefore to be searched for the nest. To heighten the chance of finding the mole-rat in its nest, the time of searching was limited to before 10.00 hr and after 18.00 hr (for reasons given later).

ACTIVITY IN *Heliophobius*

No study was made of the relationship between rainfall, soil moisture and the number of mounds thrown up by *Heliophobius*. The mole-rat used in this study was caught on the Athi plains and the danger of losing any equipment left unguarded, made it impossible to do any long-term study in the field. A compromise was made by tagging and releasing a captive *Heliophobius* into a cultivated area close to the Zoology Department, Nairobi.

Tagged Heliophobius

Adult female: weight when tagged = 165 g

Date tagged: 3 June 1969

Recordings began: 8 June 1969

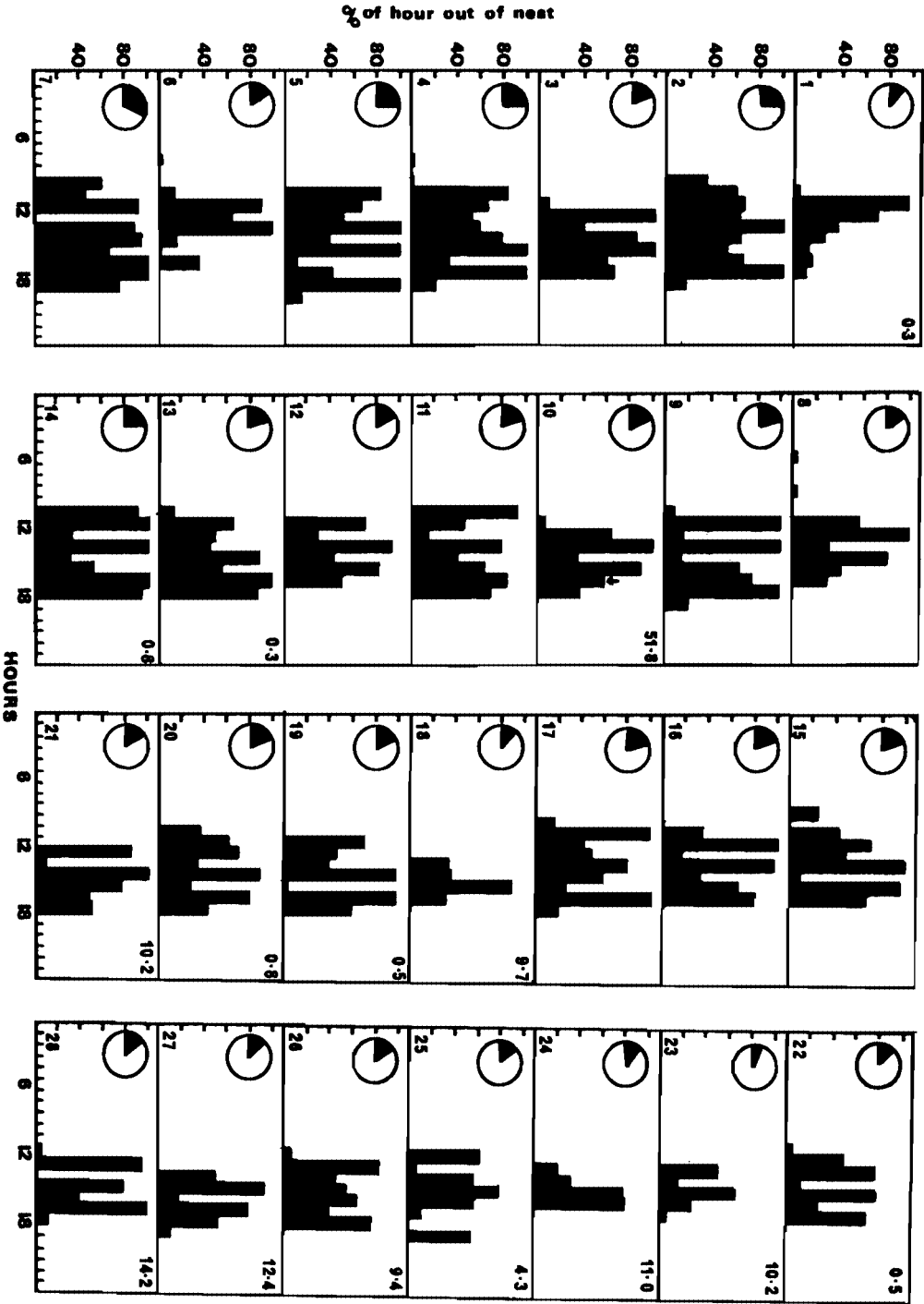
Recordings ended: 4 July 1969.

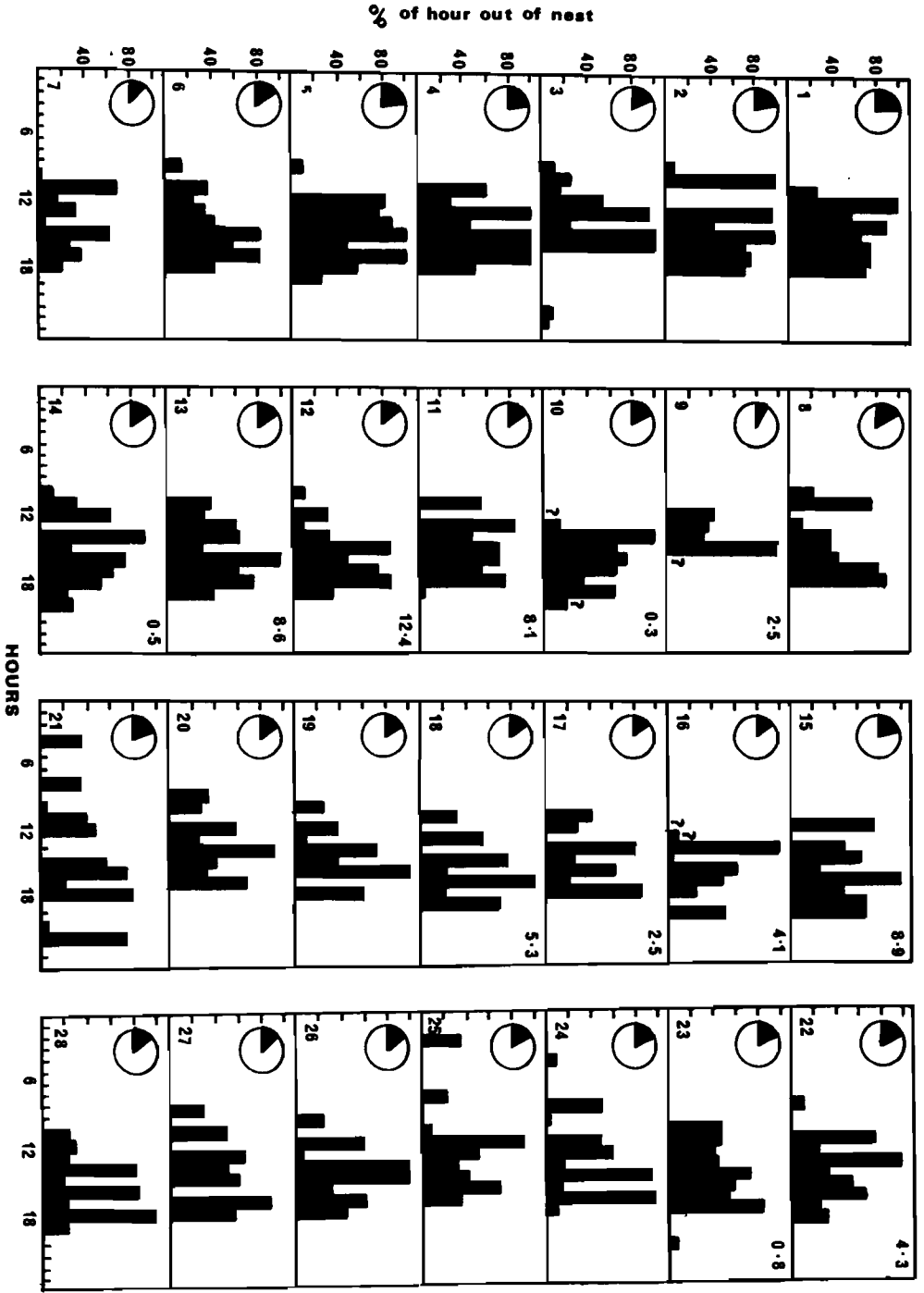
Comments: The mole-rat was recaptured and the tag removed. She appeared in excellent health and had increased her weight to 178 g. The animal was still active and healthy a year later. Details of her activity are given in Figure 8.

FIGURES 3 AND 4 (Pages 107 and 108)

Activity in *Tachyoryctes* tagged with Tantalum-182. To show the per cent of each hour and day spent away from the nest. Figure 3 shows the activity of Mole-rat B, an adult female; Figure 4 the activity of Mole-rat C, an adult male.

- (i) Histograms show the per cent of the hour away from the nest.
- (ii) Circles at the top left corner indicate the per cent of each day spent away from the nest.
- (iii) Day sequence is indicated by the bottom left-hand number (the sequence is not always without interruption).
- (iv) Rainfall (mm) is shown by the top right-hand number.
- (v) ? Indicates that no recording was made—due to technical faults in the equipment.
- (vi) ↓ in Figure 3 indicates when the first rain of the wet season began to fall.





RESULTS

MOUND-BUILDING ACTIVITY IN *Tachyoryctes*

Two types of mounds are made by adult *Tachyoryctes*. First, large mounds composed of soil excavated during burrow construction; second, small "earth-plugs" used to seal holes to the surface made when the mole-rats forage above ground (Jarvis and Sale 1971). Young animals produce small mounds which can be easily confused with the earth-plugs made by adult animals. The number of mounds and earth-plugs in the study area were recorded separately, but no attempt was made to distinguish between the latter and mounds made by young animals.

Figure 2 shows the mound-building activity, rainfall and relative soil moisture over the study period. There was a sharp increase in the number of large mounds following the first heavy rains for almost two months (late January 1969). Thereafter, the correlation between the formation of these mounds and rainfall is not distinct. Non-quantitative observations of mound-building activity over 2,5 years indicated that, had the rain pattern been normal and the heavy rain continued, the initial period of much activity would have been followed by a period of quiescence and then, as the soil dried, another burst of mound-building activity.

Also shown in Figure 2 is an increase in the number of earth-plugs produced several months after the onset of the rains. These were largely confined to one portion of the study area where, at the end of the study period, the two sub-adult female mole-rats were caught. These three-month-old animals had been born during the duration of the study; the mole-rat population in the area had therefore changed at some time during the study. Confusion between small mole-hills made by young animals and earth-plugs made by adults has probably resulted in an inaccurate record of earth-plug numbers.

It is clear that a number of factors contribute towards making this method of gauging mole-rat activity unreliable and therefore of limited value. Changes in the number and age of the mole-rats during the study period influenced the number of mounds and earth-plugs produced, and thus gave a confused impression of digging and foraging activity. Other factors such as the tendency, during the height of the dry season, to use excavated soil to block up existing burrows rather than throw it up as mounds (Jarvis and Sale 1971) and the fact that one earth-plug may be used several times, also detract from the value of using a count of mounds and earth-plugs as an indicator of mole-rat activity.

ACTIVITY OF TAGGED *Tachyoryctes**Basic activity patterns* (mole-rats B and C)

From Figures 3 and 4, it is immediately apparent that in *Tachyoryctes* there is a basic 24 hr activity cycle during which the mole-rat leaves the nest chamber for a definite period of the day. This falls between 10.00 hr and 19.00 hr; the nest is rarely left outside this period. Twenty-five per cent of the day, or less, is spent out of the nest.

Mole-rat B (Figure 3) was tagged towards the end of the dry season and recordings continued into the short rains. The mole-rat appeared to be more active when conditions were very dry than when the soil was very wet and a slight drop in activity occurred with the first heavy rain

(Figure 5). This was followed by a small increase in activity and then a decline in daily activity. Following the onset of the rains, the amount of easily accessible food would greatly increase and this could account for the decline in daily activity shown by the mole-rat. It is possible, however, that this decreased activity can be partly attributed to the accumulative effects of a prolonged exposure to radioactivity.

Also apparent from Figures 3 and 4 is the fact that frequently an hour with much activity is followed by one of comparative rest. Long periods of continuous activity out of the nest rarely occurred and the longest time spent away from the nest was when mole-rat C was out 226,5 min. (14.435 to 18.30 hr). The average period out of the nest was 37 minutes for mole-rat B and 46 minutes for mole-rat C.

In addition to this hourly rest and activity cycle, it is obvious from Figure 5 that there is also a cycle of a day of increased activity followed by a day of relative rest. A more detailed breakdown of daily activity is given later.

The basic activity of rhythms of the male and female *Tachyoryctes* was very similar. The major difference appeared to be that the male occasionally left his nest during the normally inactive hours of the day. Thus, on days 21, 24 and 25 and for shorter periods on several other days, the mole-rat was active outside the usual period. Not shown in Figure 4 is the fact that between day 6 and 7 and also towards the end of the study period, this mole-rat moved its nest to a new area. On both these occasions the move took place in the early hours of the morning (between 1.00 and 3.30 hr).

It should be stressed here that the above activity patterns only show the amount of time spent by the mole-rat away from the nest. The mole-rat must, in addition, spend considerable time feeding, grooming and defaecating when in its multipurpose nest chamber. The actual time spent in rest and sleep cannot be gauged from this study of tagged *Tachyoryctes*.

Throughout the period of recording the activity of mole-rat B, hourly air (40 cm above ground), ground and burrow temperatures were taken with a "Grant" multichannel thermister type recorder. It was found that as the ambient temperature rose, there was a slight, but corresponding drop in the burrow temperature (at burrow depths of about 25 cm). This change in temperature never exceeded 1°C over 24 hr and burrow temperature lay between 19 and 21°C over the entire study period. The drop was thought to be due to the heat from the sun causing water evaporation in the surface soil and thus cooling the earth a little deeper down. It is possible that this change in temperature, although very slight, may be sufficient to trigger activity in *Tachyoryctes*. Two factors, however, indicated that temperature was not critical, First all attempts at correlating the daily records of the time of temperature drop with the time that the animal first left the nest, were unsuccessful. Second, captive mole-rats showed similar activity rhythms to those in the wild, in spite of being exposed to large daily temperature fluctuations and a rise in temperature at the time that it drops in the burrow.

Details of daily activity (mole-rat A)

The daily activity of mole-rat A was studied in detail. On five days (not consecutive) the mole-rat was followed with a portable geiger counter, whenever it left the nest area. The time and area visited was noted and where possible the activity in which the mole-rat was engaged. The results are shown in Figure 6, a plan of the burrow system is given in Figure 7. From these two

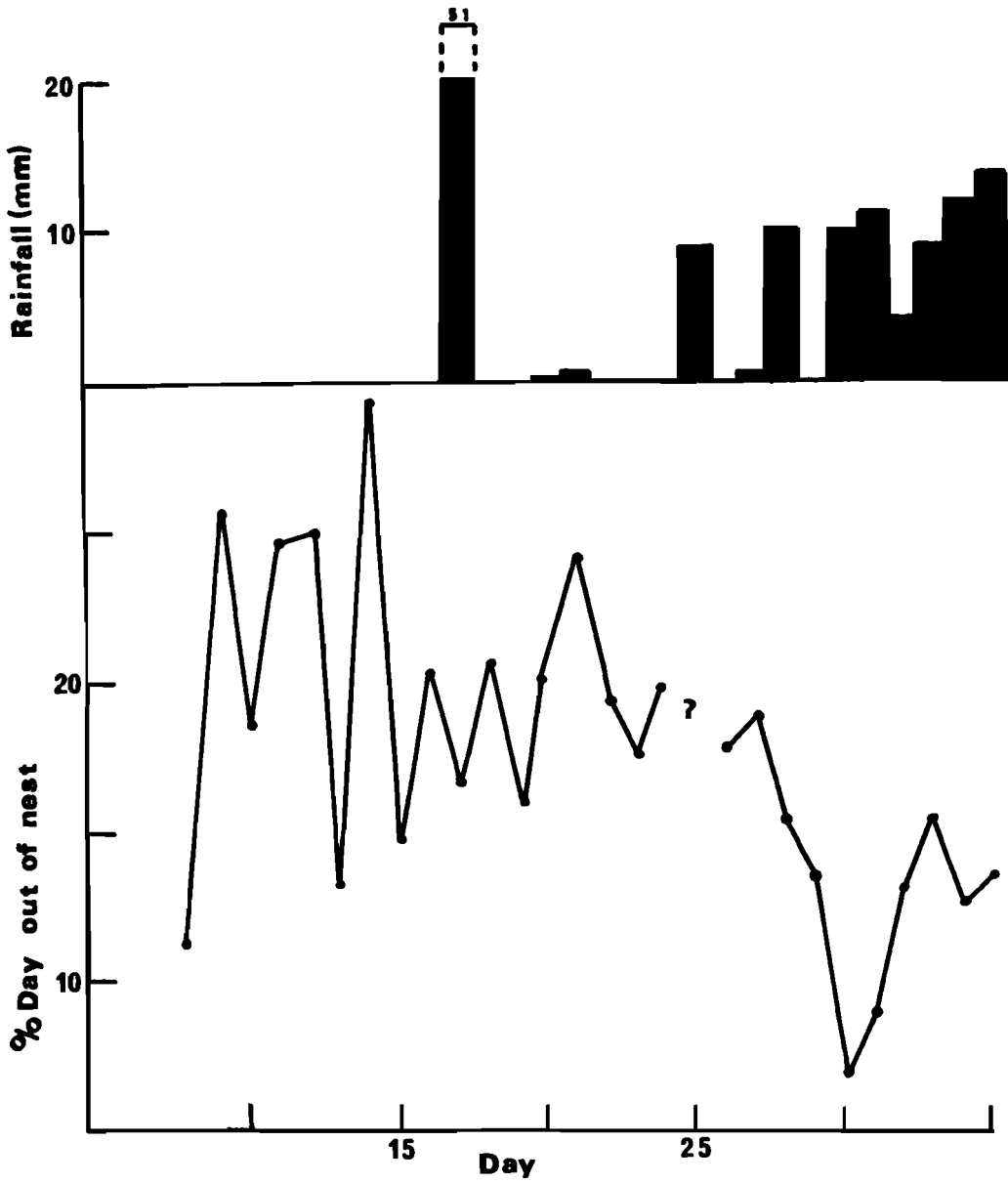


FIGURE 5

An analysis of the percentage of each day spent away from the nest of Mole-rat B. The rainfall (mm) for this period is also shown. The first 15 days show activity at the end of the dry season; days 16 to 35 show activity when the soil is wet.

figures the places visited, the length of the stay and the time of day can be seen. Uniform climatic conditions obtained throughout the study period.

A footpath ran through the area and consequently the mole-rat was familiar with the sound of footsteps. When following the mole-rat with the geiger counter, the observer walked softly and avoided producing earth-borne vibrations. As far as could be ascertained, the mole-rat was not disturbed by the presence of the observer.

Certain activities such as mound-building, foraging and feeding underground and on the surface were clearly discernible. Feeding and foraging underground were indicated by hearing the mole-rat bite or break off grass and herb roots and by seeing the aerial portion of the plants moving and portions disappearing underground. If the material taken underground was dead and dry it was assumed that this was used as nesting material. If the plant was green and immediately taken to the nest, it was probably stored as food. If, after pulling a plant underground, the mole-rat remained in the burrow close to the foraging area, it was assumed that the plant was being eaten. Surface foraging through an open hole and mole-hill formation could be directly observed.






Details for day I are incomplete, as difficulty was experienced in following and relocating the mole-rat. Thereafter, an increasing knowledge of the burrow system and also of the places favoured by the mole-rat enabled rapid re-location when she moved.

The type of activity varied considerably from day to day and frequently, on one day, one type of activity predominated over all others. Thus on days I and V long periods were spent in mound-building and in extending the foraging burrows, on days II and III foraging was the major activity. The total number of minutes engaged in each activity is given in Table I. The entire period designated to each activity was not spent in continuous activity; brief periods (less than three minutes) of inactivity and periods of less than three minutes spent away from the area are not shown.

TABLE I

A SUMMARY OF THE TOTAL TIME (IN MINUTES) PER DAY DEVOTED TO VARIOUS ACTIVITIES IN *Tachyoryctes*. DATA FROM FIVE DAYS OF ACTIVITY BY MOLE-RAT A

Type of activity	Day				
	I	II	III	IV	V
Mound building, digging	130	0	0	48	164
Foraging, feeding underground ..	24	180	110	119	44
Surface foraging	10	38	85	12	12
Other activities	62	102	73	105	69
Animal lost to observer	163	0	0	32	28
Total min. out of nest	389	320	368	316	317
% of day out of nest	27	22	19	22	22

-  Foraging & feeding underground
-  surface foraging
-  In nest
-  Mound building
-  Other activities

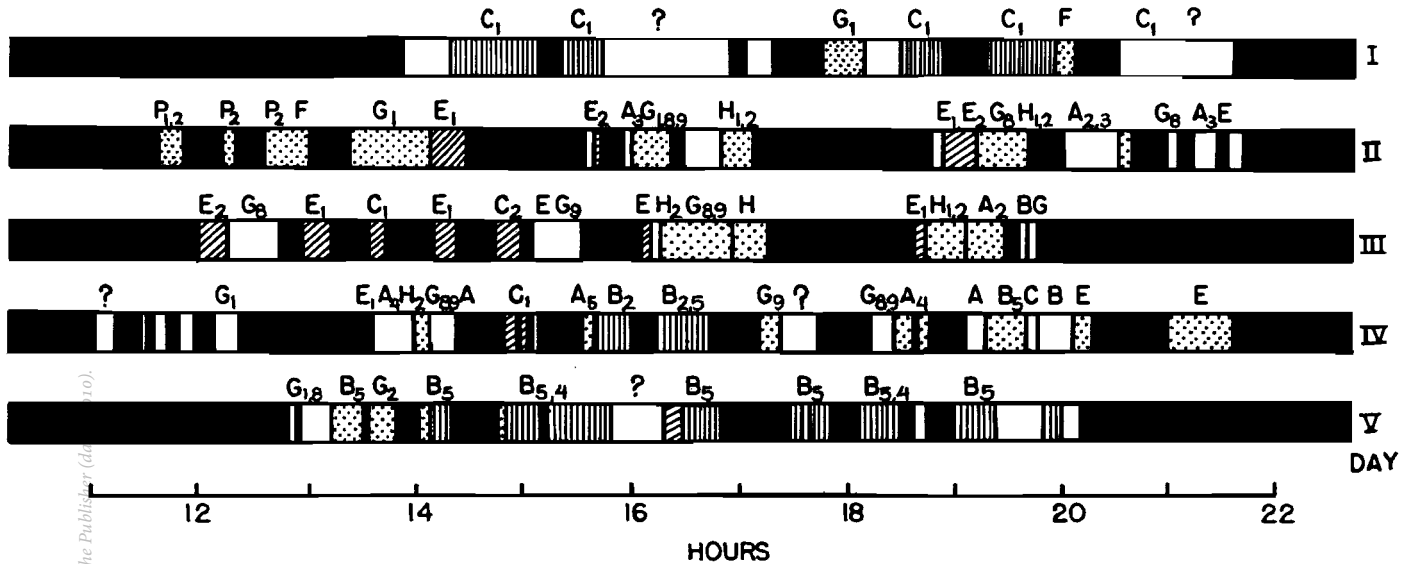


FIGURE 6

Details of the daily activity of mole-rat A. The letters and numbers above each type of activity correspond with those on the plan of the burrow system given in Figure 7 and indicate where, in the burrow system, each activity was being performed. Brief periods of less than three minutes away from the nest or away from the site of any activity are not shown. The mole-rat did not leave her nest before 11.00 hr or after 22.00 hr.

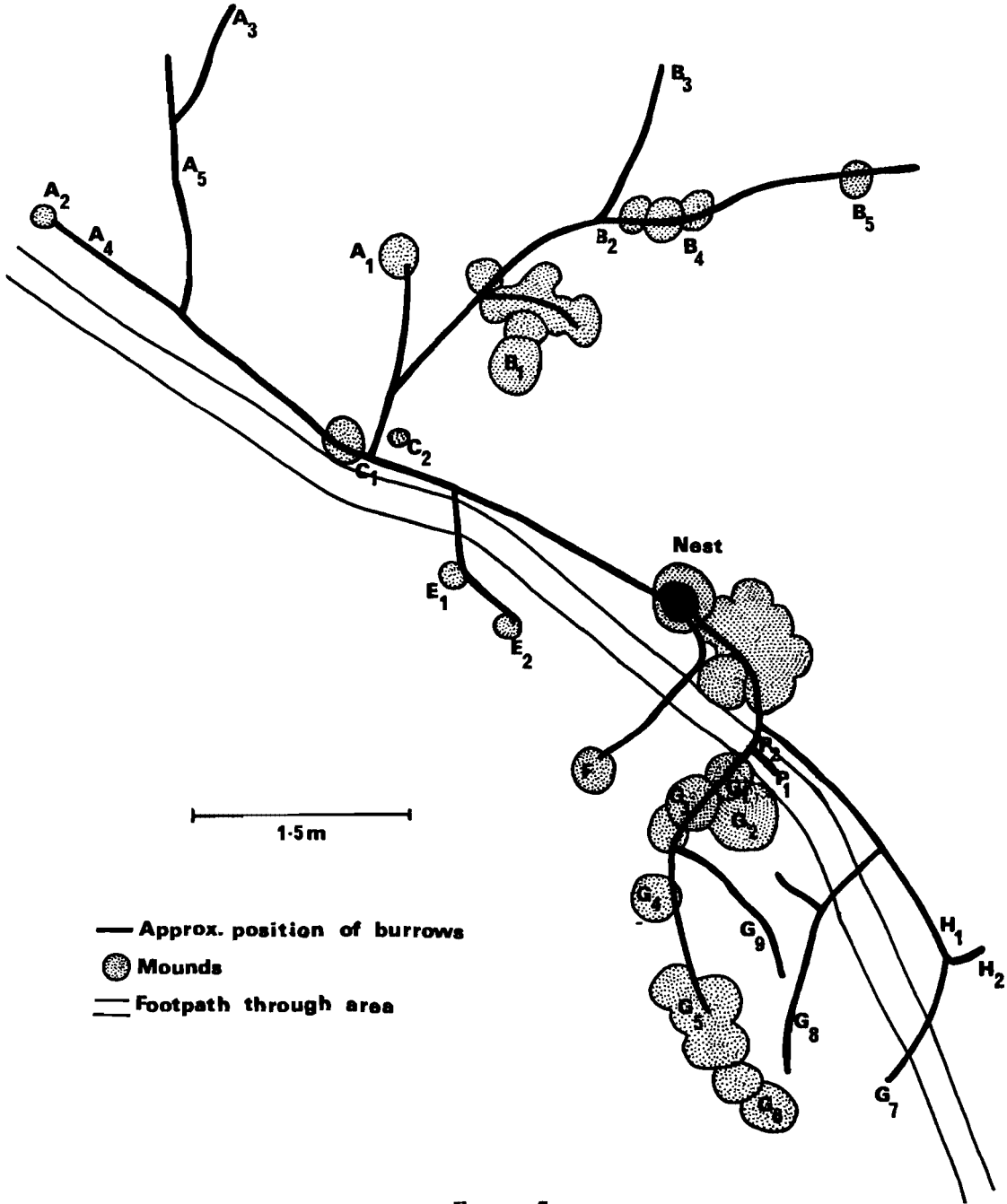


FIGURE 7

The plan of the burrow system of mole-rat A. The letters and numbers shown here correspond with those in Figure 6.

When engaged in extending the foraging burrows and disposing of the excavated soil as mole-hills, the mole-rat concentrated on one area during one day. Digging on day I was confined to the area near CI, while later excavations were in areas B2, 4 and 5. When engaged in intensive digging activities, the periods spent in the nest during the active hours were shorter than when foraging activities predominated (Figure 6). However, no greatly increased total percentage of the day out of the nest was found on digging days. The mole-rat simply devoted more time when out of the nest, to mound-building and digging and less to other activities. This may explain why, in Figure 5, the daily activity following the first rain of the season shows no increase over the pre-rainfall activity; in spite of this being the optimum time for mound-building.

Foraging activities were two-fold. Most frequently, the mole-rat removed the soil round the base of a plant and bit through the roots and leaf and stem bases. As mentioned earlier, this could be plainly heard by an observer standing near the mole-rat. Once a leaf or stem base had been severed, the mole-rat seized it and pulled the aerial portion underground. If very long, part of the plant would be pulled under and a manageable piece bitten off, carried to the nest and then a second piece removed. This frequently occurred with long pieces of the grass *Panicum maximum*. At no time during this foraging was the mole-rat exposed although it was often very close to the surface. Materials pulled into the burrow in this way, and also with surface foraging (see later), were often taken straight to the nest. Occasionally the animal gathered a number of pieces before taking them to the nest chamber. A long pause in foraging activities with the mole-rat stationary just below the area being foraged indicated that the mole-rat was feeding, and possibly resting, away from the nest.

A second method of collecting food and nest materials was through surface foraging. Areas C and E were favoured for this activity. Here, the mole-rat opened a small hole to the surface and partly emerged to collect plants above ground. Great caution typified this activity. The mole-rat frequently spent five or more minutes sniffing the air with only her nose exposed. Any loud sound would make her disappear completely. If undisturbed, the mole-rat would eventually emerge with short jerky movements and uttering soft snorts. With little more than half her body out of the hole, the mole-rat would suddenly jerk forwards, seize a piece of vegetation with her incisors and dart backwards into the burrow. This sudden retreat would sever the piece seized from the parent plant. The mole-rat was never seen to completely leave the burrow, although other *Tachyoryctes* were occasionally found wandering above ground.

Study of the behaviour of a captive animal foraging in an earth-filled glass tank showed that during surface foraging the hind feet are kept in the burrow and are braced for rapid retreat should the need arise.

At the end of surface foraging or if disturbed by a loud noise, the mole-rat plugged the foraging hole with an earth-plug. After a period ranging from a few minutes to more than one day the same hole may be unplugged and foraging resumed.

The following plants were taken underground by the foraging mole-rat: the grasses *Panicum maximum*, *Sporobolus filipes* and *Chloris pynothrix*, the herb *Galinsoga parviflora* and the creeper *Zehneria scaba*. All were common in the study area.

It is difficult to ascertain the reason for surface foraging. This may be a labour-saving device whereby the mole-rat can reach vegetation without having to expend energy in extending a foraging burrow. However, in this particular burrow system much potential food, growing

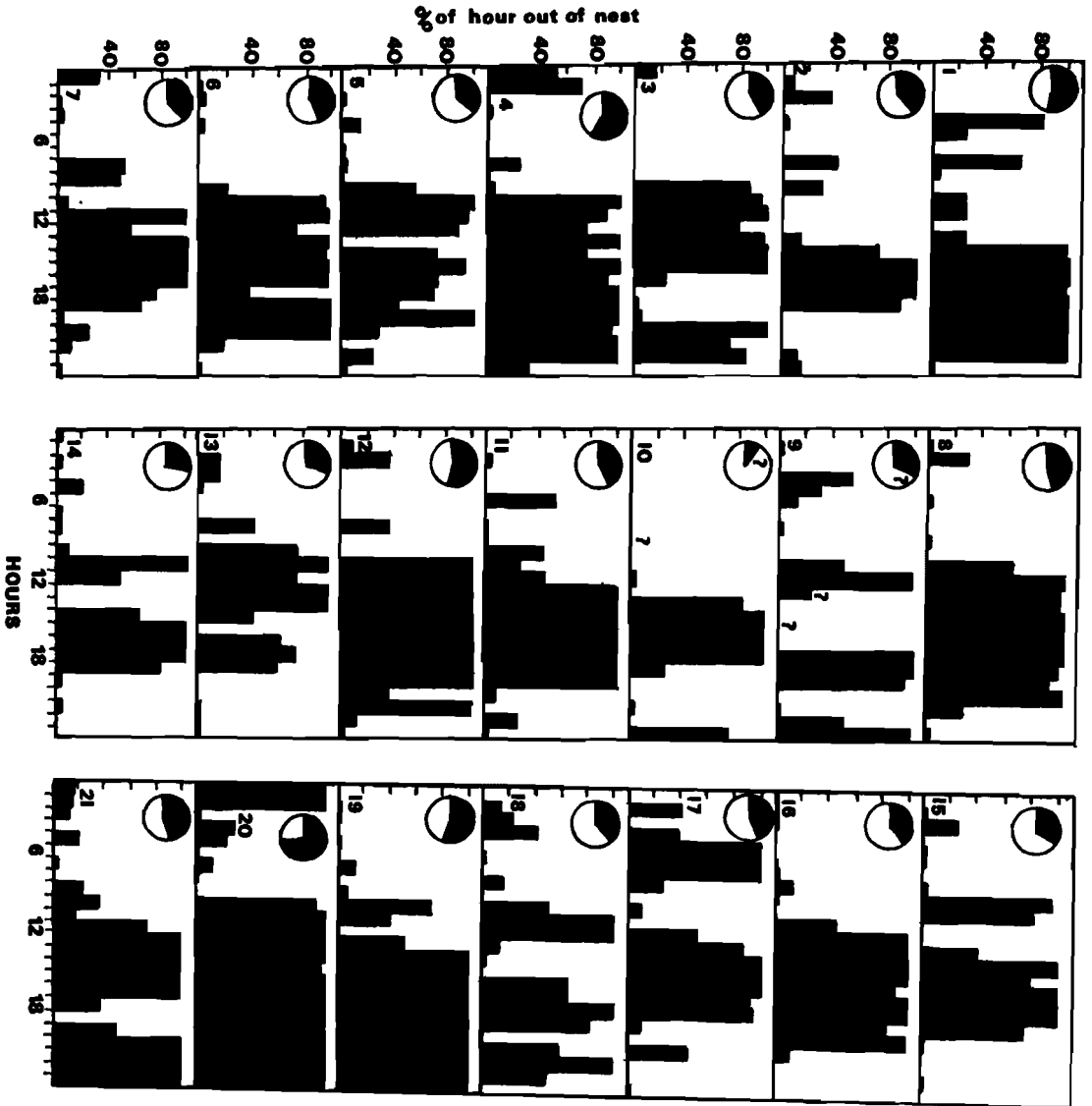


FIGURE 8

Activity in *Heliophobius* tagged with Tantalum-182. To show the per cent of each hour and day spent away from the nest. See the legend for Figures 3 and 4 for explanation.

above already excavated burrows, was available to the mole-rat. There therefore appeared to be little need to come to the surface and be exposed to the dangers of foraging out of the protected burrow. Whatever the reason behind this activity, it occurred frequently and must be of importance.

ACTIVITY OF TAGGED *Heliophobius*

The relationship between rainfall and the number of mounds thrown up by *Heliophobius* was not studied. Genelly (1965) showed that there was a clear link between soil moisture and the digging of foraging burrows in *Cryptomys* and the same is probably true of *Heliophobius*. Like *Tachyoryctes*, *Heliophobius* was found to block some of its foraging burrows with excavated soil during the height of the dry season and consequently few fresh mole-hills were found when the soil was dry.

The basic activity pattern of the tagged *Heliophobius* is given in Figure 8. It is immediately obvious that *Heliophobius* spends more of the day out of the nest than *Tachyoryctes* (over 50 per cent of the day). Activity occurs at any time of the day, but is greatest between 9.00 and 22.00 hr. Long continuous periods are spent away during peak active hours. On one occasion (days 19 and 20), 13 hours and 32 minutes were spent continuously away from the nest.

Several factors may have influenced the activity pattern of the mole-rat. These included the fact that the animal had been captive for two years and was released into an area not normally inhabited by *Heliophobius*, where the soil type was different and the temperature lower than that of its natural habitat. In addition to this, the mole-rat was not released into an already established burrow system and consequently had to dig its own system of burrows. Much of this was done during the first four days after release (as shown by the production of mole-hills) when no record of her movements was made. An extensive burrow system was not necessary because the mole-rat had been released into an area planted with carrots and sweet potatoes and therefore had an abundant food supply. Small extensions to the burrow system were made throughout the study period but the number of mounds produced was not greatly in excess of those produced by the tagged *Tachyoryctes*. The sparsity of data on the activity of fossorial mammals justifies, in the author's opinion, the inclusion of these somewhat inadequate results in this paper. It is suggested that in spite of these possible sources of error, the activity patterns of *Tachyoryctes* and *Heliophobius* are significantly different.

No detailed study was made of the daily activity of *Heliophobius*. It is not known how the periods away from the nest are spent. Mound-building activity appeared to be more frequent between 15.00 and 18.00 hr. On days 4, 19 and 20 much mound-building occurred but the mole-rat was out of the nest at other times of the day probably for feeding.

After the mole-rat was recaptured, the nest area was examined to verify that this was indeed the nest and not a place frequented by the mole-rat for some other reason. It was found to be a chamber containing grass nesting materials and fragments of sweet potatoes and carrots.

DISCUSSION AND CONCLUSIONS

The discovery of a distinct daily activity pattern in *Tachyoryctes* is surprising. These mole-rats live in an environment where light, temperature, humidity and the availability of food show little

daily fluctuation. In spite of this, *Tachyoryctes* confines its period of activity out of the nest to a clearly defined time of the day. It also appears from the limited data available, that male and female *Tachyoryctes* show similar activity patterns although the male does occasionally deviate from this pattern. There is no apparent seasonal change in the activity pattern. The advantages gained by *Tachyoryctes* in restricting its foraging activities to a specific time of the day are difficult to assess.

Prior to this study on activity it was suspected, largely because few mole-hills were produced, that *Tachyoryctes* aestivated during the height of the dry season. Captive *Tachyoryctes* occasionally went into a deep sleep in which they could be handled without waking, this again suggested that aestivation occurred. The study of activity in Mole-rat B, during the dry season, showed no sign of such inactivity. Lack of aestivation is also indicated by the fact that mole-rats can be caught throughout the year and that breeding occurs over both the dry and wet times of the year (Jarvis 1969).

Two reasons for the difference in the activity patterns of *Tachyoryctes* and *Heliophobius* are immediately apparent. Experiments by Eloff (1958) indicate that bathyergids cannot distinguish light and dark, my own observations bear this out. *Tachyoryctes* on the other hand has larger eyes which appear to be photosensitive. Activity in *Heliophobius* is therefore probably geared to the internal requirements of the mole-rat and not directly to some external factor such as light. Ashby (1972) points out that under natural conditions, the entrainment of the daily activity rhythm in many mammals appears to be caused by the periodicity of rapid change in light intensity (i.e., dawn and dusk). It is suggested that the brief exposures to light experienced by *Tachyoryctes* during surface foraging activities, particularly when the mole-rat forages at dusk, acts as a trigger for the 24-hr activity rhythm found in these mole-rats. This brief exposure above ground is, indeed, the only time that there is any marked change in the otherwise uniform conditions under which *Tachyoryctes* lives.

The second factor leading to the differences in activity patterns in the two mole-rats can be linked with the function of the nest chamber in the two genera. *Tachyoryctes* has a large multipurpose nest chamber in which feeding, sleeping, and defaecation take place, whereas *Heliophobius* has a nest used solely for rest. Elton, Ford, Baker and Gardner (1931) pointed out that mice have a short-term cycle of feeding, recurring every few hours, the interval being determined by the stomach volume and rate of digestion of the animal. This short-term rhythm within the overall daily periodicity has been shown to occur in many small rodents and insectivores (Ashby 1972). Observations of the feeding times of captive mole-rats showed that both *Tachyoryctes* and *Heliophobius* fed at irregular intervals throughout the day and night (Jarvis, unpublished). In the field, this activity in *Tachyoryctes* would be almost entirely confined to the multipurpose nest. It was therefore not recorded by the methods used in this study. With *Heliophobius* on the other hand, the mole-rat had to leave its nest to feed and therefore this activity was recorded. It was not possible to differentiate this short-term activity from the basic 24-hr activity pattern of this mole-rat and the two are superimposed in the record obtained in this study. It is possible that the periods spent by *Heliophobius* out of the nest during non-peak activity hours, are solely for feeding and defaecation. More sophisticated recording methods may possibly show that the major difference between these two mole-rats is not the duration of their activity but the place in the burrow system where these activities occur.

It is, of course, possible that some of the differences in behaviour between these two families can also be attributed to their different phylogenetic affinities.

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REFERENCES

- ASHBY, K. R. 1972. Patterns of daily activity in mammals. *Mammal Rev.* 1(7/8):171-185.
- DE GRAAFF, G. 1968. Rodentia: Bathyergidae. *Smithsonian Inst. Preliminary Identification Manual for African Mammals* Part 16.
- ELOFF, G. 1958. The functional and structural degeneration of the eye of South African rodent moles *Cryptomys bigalkei* and *Bathyergus maritimus*. *S. Afr. J. Sci.* 54(11):293-302.
- ELTON, O. S., FORD, E. B., BAKER, J. R. & GARDNER, A. D. 1931. The health and parasites of a wild mouse population. *Proc. zool. Soc. Lond.*, 657-721.
- GENELLY, R. E. 1965. Ecology of the common mole-rat (*Cryptomys hottentotus*) in Rhodesia. *J. Mammal.*, 46(4):647-665.
- GODFREY, G. K. 1955. A field study of the activity of the mole (*Talpa europea* L.). *Ecology* 36: 678-685.
- INGLIS, J. M., POST, L. J., LAHSER, C. W. & GIBSON, D. V. 1968. A device for automatically detecting the presence of small animals carrying radioactive tags. *Ecology* 49(2):361-363.
- JARVIS, J. U. M. 1969. The breeding season and litter size of African mole-rats. *J. Reprod. Fert., Suppl.* 6:237-248.
- JARVIS, J. U. M. & SALE, J. B. 1971. Burrowing and burrow patterns of East African mole-rats *Tachyoryctes*, *Heliophobius* and *Heterocephalus*. *J. Zool., Lond.* 163:451-479.
- MISONNE, X. 1968. Rodentia: Main text. *Smithsonian Inst. Preliminary Identification Manual for African mammals.* Part 19.