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CHRONOLOGICAL DEVELOPMENT OF BEHAVIOR IN THE BLIND MOLE RAT (*SPALAX EHRENBERGI*)

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ABSTRACT: The blind mole rat (*Spalax ehrenbergi*) is a potentially highly aggressive solitary, subterranean rodent. Data on growth and development of pups are lacking since it is difficult to raise pups in captivity and, until recently, the blind mole rat has never bred in captivity. In this study six litters were maintained in six large semi-natural set-ups. We describe for the first time the chronological development of behavior in the blind mole rat from day of birth until the young disperse and establish their own independent territories. The relatively short gestation period (34 days) and low birth mass (5-6 g) combined with the need to acquire all survival skills prior to dispersal, are probably correlated with the relatively lengthy development of the blind mole rat compared to Bathyergidae.

The blind mole rat (*Spalax ehrenbergi*) is a highly aggressive, solitary, subterranean rodent. These characteristics make it difficult to maintain and breed in the laboratory and most past attempts to breed this species in captivity have failed (Nevo, 1969; Shanas *et al,*1995); the first successful attempt occurred only recently (Gazit, Shanas & Terkel, 1996). Consequently, little is known about growth and development of mole rat pups. The blind mole rat breeds once a year in the winter although recent evidence has shown that it also appears to have the potential for summer breeding (Shanas *et al,* 1995; Gottreich *et al,* 1995; Zuri and Terkel, 1996). Litter size ranges from 1-6 young (3-4 on average), weighing 5-6 gram each (Nevo, 1961). The pups are born naked and become covered with fur by the age of two weeks, when they also begin to move about the nest area.

The only aspect of behavioral ontogeny which has been studied in

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the blind mole rat is the transition from vocal to seismic communication in wild caught pups and its correlation with the shift from social to solitary life style (Rado, Wollberg & Terkel, 1991; Rado, Wollberg & Terkel, 1992).

The behavioral and physiological development of species of subterranean rodents of the family Bathyergidae, has been studied and widely reviewed by Bennett *et al* (1991). In contrast, little is known about the behavioral development of North and South American subterranean rodents since most studies have been based on post-mortem measurements. Andersen (1978), in particular, has described the development of the Pocket gopher (*Thomomys talpoides*).

In the present article we describe the behavioral development of the blind mole rat from the day of birth until the young disperse and establish their own independent territories. We particularly focus on the development of motor activity; establishment of separate food storage; sparring, and the increasing aggression between mother and young and among siblings associated with the transition from social to solitary life style.

METHOD

Subjects

Eleven mole rat pups (6 males, 5 females) from six litters were studied. Three of the litters were conceived and born in captivity during this study; one pregnant female was captured in the field and gave birth in the laboratory; and two mothers with 1-2 week old litters were caught in the field and brought to the laboratory. The study lasted for three breeding seasons, i.e. three years.

Procedure

Each of the six mothers and their litters were placed in a separate experimental set-up (Figure 1), comprising five transparent plastic cages (22x43x13 cm) interconnected by transparent Perspex tubes (total length of 9 m, 54 mm inner diameter, ca. the diameter of an adult mole rat body). Each cage contained damp soil 10-15 cm deep, enabling the mole rats to dig tunnels and block the borders of their territories. The wire mesh cage lids were covered with a clear Perspex sheet preventing air flow over the system while enabling observation of the events

within the cages. This set-up thus modeled a natural tunnel system, with separate functional chambers and completely closed to external air flow. Removable screw barriers inserted in the tubes, separated the system into two sections (Figure 1) but allowed free access to both sides by the small sized young while restricting the mother to one section.

Room temperature ranged between 25 ± 2°C in summer and 19 ± 3°C in winter, and lighting was provided by natural light from a window.

Animal care was designed to cause the least possible disturbance. Food and nesting material were introduced twice weekly into the cage not used by the mother for her nest and into one cage in the pup area. The food provided included fresh green grass and oxalis bulbs (*Oxalis cernua*) that comprise a large part of the mole rat's diet in nature, as well as apples, carrots, lettuce, sunflower seeds, and peanuts. The cages were cleaned at approximately ten day intervals, focusing predominantly on the toilet area.

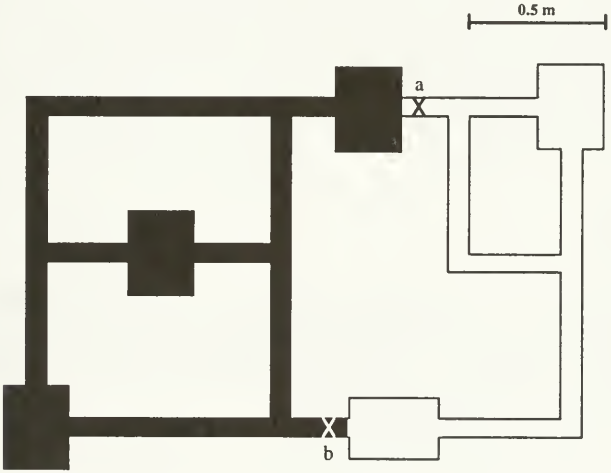

Figure 1. Schematic representation of the experimental set-up, showing the area available to the mother (black) who is too large to pass through the screw barriers (a,b), while the entire set-up (both areas - black and white) is available to the young.

Measures

Direct daily observations of each individual pup took place over 4-5 months, beginning on the day of birth or capture. Each observation lasted for two hours during the animal's active period.

In order to obtain a complete picture of the ontogeny of mole rat pups' behavior, twenty four different behavioral acts were recorded, in the chronological order in which they appeared. A brief description of the behaviors is presented in the results (see Table 1). In addition to the chronological development of behavior, detailed quantitative and qualitative data were collected from two siblings: male and female. Since it was impossible to perform such detailed observation on a larger number of pups, within the limits of this study, and based on previous observations in which we had found that there may be sex based differences in behaviors, the present study specifically selected a litter that contained one pup of each sex.

The types of functional categories of behavioral acts which we observed were: *Motor activity*; duration (in min) of pup activity throughout the observation period (excluding sleep); *Communication;* including chirps, jaw listening and head drumming, measured as number of events per time unit; *Play*; between pups (in min.) and *Interaction with mother or sibling;* either (a), when the two animals were in the same side of the set-up most of the interaction comprised playing or fighting or (b), when they were separated by the screw barrier the interaction comprised mainly building and dismantling the soil barrier, sniffing one another or gnawing at the screws.

RESULTS

Table 1 summarizes the chronological order of first appearance of each behavior pattern. By grouping the developing behavioral acts according to functional categories a more complete picture emerges of the progression toward adult behavior.

Motor activity

The pups began wandering around the nest at about two weeks. Until age 3-4 weeks, the mother would retrieve the pups to the nest by gently grasping almost any part of their body in her teeth. At six weeks the pups walked through the entire maternal tunnel system for the first time. The young mole rats usually walked with their noses in contact with the roof or floor of the tube. Reverse (backward) walking, used as frequently as forward walking by adult mole rats, first appeared at an age of five weeks on average; this behavior occurred even though the pups were still easily able to turn around inside the tubes and continue forward walking.

Table 1. Chronological appearance of behavior during development of mole rat pups.

Behaviors	Age	SE
Wandering out of nest into adjacent tube	14.5	0.2
Eating solid food in the nest area	20.7	2.3
Gathering food and carrying to mother's nest	31.3	4.4
Grooming head with forepaws	31.8	1.2
Backwards walking in tunnel	32.5	3.0
Use of maternal toilet for excrement	33.0	3.0
Scattered digging in soil in maternal cages	34.6	1.4
Jaw listening[1]	35.6	1.6
Play between pups	36.7	5.5
Wandering through the entire maternal tunnel	38.3	0.9
Teeth baring: exposure of incisors without biting	41.0	4.0
Weaning	44.0	2.0
Forming separate food storage from mother	45.4	5.4
Gathering nesting materials to mother's nest	49.5	8.3
Aggression between pups: teeth baring, biting, squeals	52.7	4.1
Head drumming[2]	56.5	5.3
Forming separate nest from mother	62.9	3.1
Aggression between mother and pups	64.5	5.1
Sleeping in separate nest during day	64.8	4.3
Sleeping in separate nest during night	66.4	14.9
Expulsion from maternal territory	70.3	4.6
Forming soil barrier at border with maternal territory	75.0	7.9
Duet head drumming between mother and pups	75.0	10.0
Urinating on soil barrier	102.0	24.0

[1]pressing lower jaw against tunnel wall to perceive vibrations

[2] the production of vibrations by tapping the head against tunnel ceiling

Food storage

During their first month, the pups spent almost all their time in the nest. The first three weeks were characterized by intensive maternal care, in which a significant portion of the mother's time was spent nursing the pups (Figure 2) and the mother stored food both in the nest area as well as in the food store. At 4-6 weeks, when the pups spent longer periods out of the nest, the female moved all the food items to the food store. At this stage the female began to seize food aggressively

from any pup that ate in the nest cage. At five to seven weeks, the pups began to gather and sort food items by type and arrange them in the mother's food store; and from seven weeks each pup began to create its own food store in the pup section of the set up. From age seven weeks until dispersal the pups gathered food for their own store as well as for their mother's. The frequency of food gathering to the mother's store was 0.3 ± 0.1 events and to the pups' store 2.8 ± 0.8 events, for 30 min. of observation (Mann Whitney U test, $p < 0.05$). Sex differences in food store location and formation were observed in three different litters: while forming their own food storage, the male pups stored only food items that were found in the pups' section, while female pups removed food items from the mother's food storage area into their own. This behavior stopped after two days when the mother became aggressive toward the female pups, which then ceased entering the mother's territory.

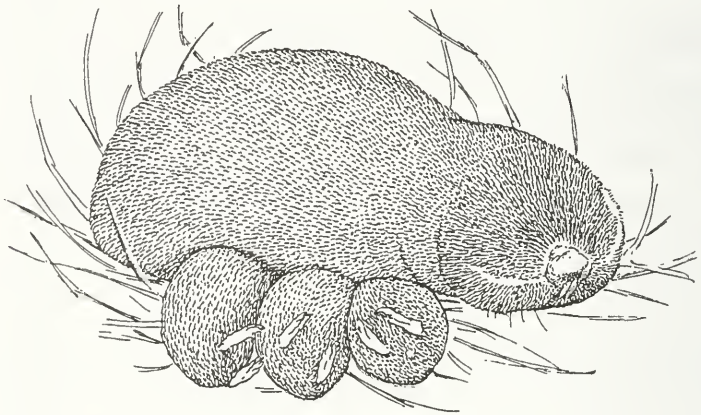

Figure 2. Female mole rat nursing her three pups. Drawing by Mr. W. Ferguson.

Play and Fighting

Play and fighting could be differentiated by several criteria: when playing the mole rats appeared relaxed and calm, their movements were gentle, smooth and slow, including gently locking their incisors, pulling and pushing each other and rolling together anterior - posteriorly. Play usually ceased suddenly when the mother approached or when the pups found a piece of food. The pups sometimes used their forefeet to push each other's head with one lying on its back and the other standing nearby. In nonaggressive play there were no bites or chirps.

In contrast, during fighting the animal's movements were quick and sharp, and accompanied by frequent short retreating jumps, often triggered by noise or movement in the vicinity. During fighting the mole rats primarily bit their opponent's body with their incisors and did not use their forefeet to push at each other, but stood on all four feet facing one another in a complete defense posture. Unlike play, the fights did not end suddenly as a result of exogenous stimuli such as nearby food; and during a serious fight it was difficult to separate the animals.

Sparring amongst pups began at six weeks and the aggression level (including bites, fights and chirps) gradually increased. At age 8-9 weeks most of the sibling interactions ended with fights and chirps. Since chirps are emitted by pups almost exclusively as a result of maternal or sibling aggression, the number of chirps emitted by the pups gave a good indication of the level of aggression. An increase in aggression was correlated with an increase in the number of chirps ($r^2 = 0.6$, $p = 0.0004$). Although the interaction length between pups did not change throughout maturation, the nature of the interaction changed to a more aggressive one at around age two months, as expressed by a sharp increase in chirps (Figure 3). Although aggression was frequent at this stage, most of the interactions between the pups did not develop into severe fights and eventually the pups went to sleep together in the mother's nest.

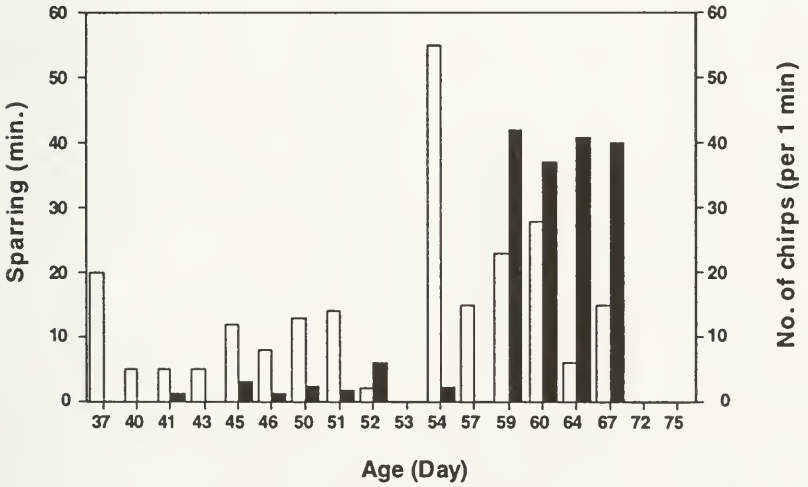

Figure 3. Duration of sparring between pups (white), and frequency of chirps (per min) emitted by the pups while sparring (black).

The presence of the mother played a major role in reducing the growing pups' aggression. As long as there was a possibility of physical contact between mother and young, aggression was suppressed. As soon as the young moved or were removed to separate territories, after reaching dispersal age, the full range of aggression was immediately expressed.

Mother - pup interaction

At the age of seven weeks, the mother started to play - fight with the pups: pushing, baring teeth and biting them gently. Although this interaction was characterized by fight elements it was of a playful nature since the pups remained calm and quiet and did not chirp or try to escape. These interactions gradually became more aggressive and the pups began to chirp more frequently when bitten by the female and frequently retreated to the nest or to the pup section of the apparatus.
During the establishment of the pup's independent territory, the interaction between mother and pup was characterized by mutual sniffing, gnawing at the screw barrier with their incisors, and pushing soil from one side of the barrier to the other. Throughout such interactions the pup chirped almost constantly.

The gender of the pup appeared to affect the total duration of interaction with its mother. Interactions between mother and male pup were significantly longer than between mother and female pup (Mann-Whitney U-test, $p < 0.01$). While the duration of interaction between mother and male pup increased after dispersal compared to before dispersal (Mann-Whitney U-test, $p < 0.01$), it decreased between mother and female pup after dispersal compared to before dispersal (Mann-Whitney U-test, $p < 0.05$) (Figure 4A). These interactions continued until the mole rats had formed a permanent soil barrier at the screw barrier area, separating the two territories. Following completion of the soil barrier, interactions decreased sharply and were limited to head drums and urination on the soil barrier.

Maternal aggression was expressed by attacking the pups with bared teeth and occasional bites, causing them to retreat to the nest while chirping. Throughout the entire period, maternal aggression was significantly higher toward the male compared to the female pup (Wilcoxon signed rank test, $p < 0.01$). From the age of eight to nine weeks, the male pup chirped every time the mother approached even when there was no physical contact between them. The female pup voiced fewer chirps than the male for the entire period. The frequency of vocalization decreased after dispersal for both the male (Mann-

Whitney U test, $p < 0.001$) and the female (Mann-Whitney U test, $p < 0.001$) (Figure 4B). After dispersal, when there was no physical contact between mother and pups, the pups' earlier high, sharp and loud chirps of fear were replaced by more drawn out, calmer chirps.

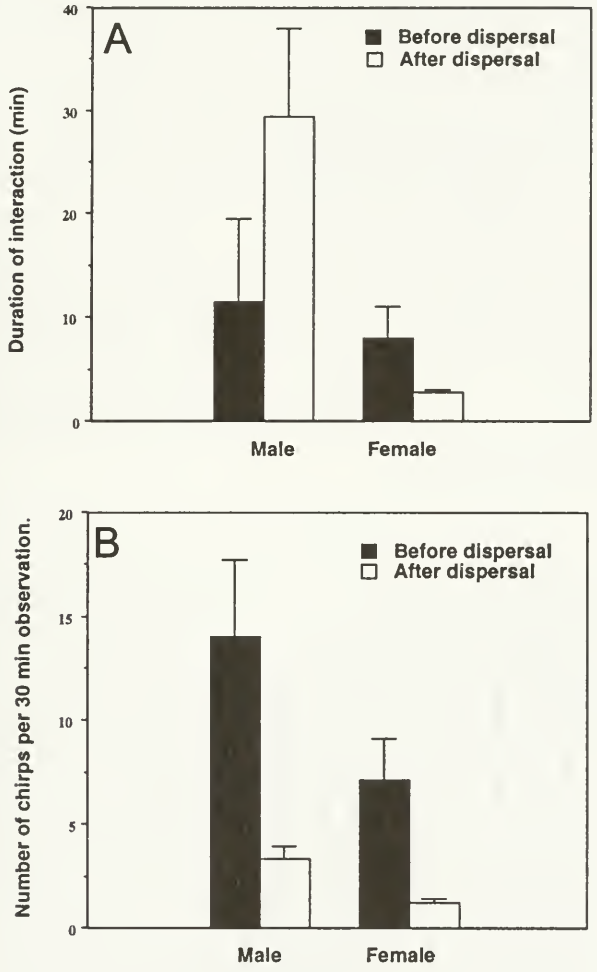

Figure 4. Interaction between mother and pups, when both resided in the mother's territory (black bars) or when the pups remained in their own territory (white bars) and were separated from their mother by the screw barrier. A, Duration of interaction (mins) between mother and pups and B, Number of chirps emitted by the pups during interactions with the mother.

Digging and establishment of a separate territory

Digging activity appeared very early in life, immediately after the appearance of vital behaviors such as independent eating and walking. At around five to six weeks the pups began to dig indiscriminately inside the mother's territory cages; while at eight weeks they were already digging straight tunnels inside the cages and pushing soil in the tube partitions.

The pups' exploration and use of the separate tunnel system adjacent to the mother's territory was gradual. At the beginning the pup blocked most of the available tubes with soil, using only a small part of the adjacent tunnel system. During the first week of territory establishment, the pups remained mainly in their own section, briefly returning to the mother's territory every 1-5 min. They gradually extended the time spent in the adjacent tunnel system, although still feeding from the mother's food storage and sleeping in the mother's nest. At the age of 11-12 weeks the pups dismantled the soil barrier that restricted the new territory length, and began to use the entire available tunnel. The young mole rats fully dispersed from the maternal territory at age 12 weeks (Figure 5).

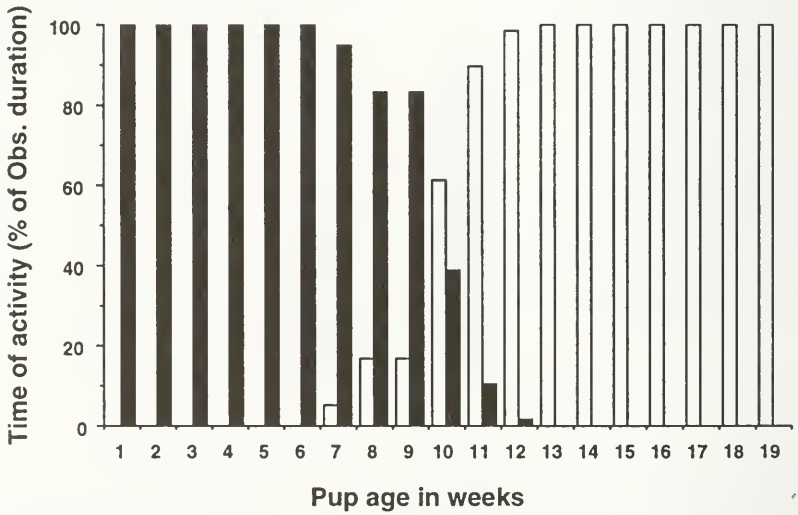

Figure 5. Percent of observation period that the male pup was present in the maternal territory (black) and in the separate territory (white).

The experimental apparatus used in our study had space for only one separate territory in addition to the mother's. In each of the five cases where there were opposite sex siblings, the male pup established his independent territory in the separate area. The female pup remained in the mother's territory for several weeks longer until a third section was added to the apparatus, or she was removed due to excessive maternal aggression.

During the establishment of their separate territories, when the pups returned to the mother's territory they pushed a small amount of soil onto the screw barrier separating the two territories. This behavior was observed 8 times for the male and 11 times for the female pups.

Elements of nest construction first appeared in four to five week old pups when they repaired the mother's nest. Approximately three weeks later, each pup began to build its own nest inside the maternal territory. At age 9-10 weeks, the male pup formed its own nest in the adjacent tunnel system, and one to two weeks later he was fully independent and rarely returned to the mother's nest.

Vocal and seismic communication

Detection of vibrations by jaw listening behavior was first performed at age five to six weeks, whereas the production of vibrations by head drumming was first performed only at age eight to nine weeks.

Head drumming increased significantly throughout the dispersal process of the pups; mean frequency of pup head drums in the maternal territory was 1 ± 0.4, compared to 6 ± 1.3 in the adjacent tunnel system, (per 30 min. of observation, Mann Whitney U test, $p < 0.01$). The same pattern also occurred with jaw listening; frequency of jaw listening performed by the pups in the maternal section was 2.2 ± 0.4, while in the pup section it increased to 8 ± 1.3 (for 30 min of observation, Mann Whitney U test, $p = 0.01$).

Duets of head drumming between siblings or between pup and mother occurred only when the two animals were separated by the screw barrier. Most of the duets occurred between mother and male pup, although occasionally we observed a trio between mother, male pup and female pup.

DISCUSSION

The seasonal semi-arid climate in Israel poses some challenges to the subterranean life of the blind mole rat. The young mole rat must be

able to dig and establish its own tunnel system, defend it against intruders and gather an adequate amount of food items during the short period between establishing independence in the spring and the summer when the soil is dry and digging is difficult. Consequently, the young mole rat is selected to disperse from the maternal territory only when it is physically and behaviorally fully developed. The short gestation period (Gazit *et al,* 1996) and low birth weight (Nevo, 1961) of the blind mole rat compared to other solitary subterranean rodent species (Jarvis, 1969; Bennett & Jarvis, 1988; Bennett *et al,*1991; Jarvis & Bennett, 1991) except the pocket gopher (Andersen, 1978), are compensated for by the proportionally longer period of behavioral development from altricial infancy to independent maturity. During this developmental period, the young acquire strength and performance skills vital for survival.

The young of social species of mole rats (family Bathyergidae) which remain in the maternal tunnel system and are incorporated into the colony, benefit from the co-operative foraging activities of adults in the colony. Thus, the selection pressures acting on them are probably different from those acting on solitary mole rats (Bennett *et al,* 1991).

The need to establish an independent territory and to defend it against intruders is correlated with the development of aggression before the young disperse from the maternal territory. Sparring between pups, beginning at age 5-6 weeks, is the first stage of practice fighting. Although the differences between play and fighting are clear, both are characterized by many of the same elements of behavior, albeit more gentle during play. Gradually, aggression between pups increases until real fights begin at age 7-8 weeks, as occurs in all solitary genera of the family Bathyergidae (Bennett *et al,* 1991) and the pocket gopher (*Thomomys talpoides*) (Andersen, 1978). During the next period of 4-5 weeks, while still in the maternal territory, the pups practice the required skills for independent life including tunnel digging and repair, food gathering, nest construction and the use of seismic communication. These skills are applied afterwards when the pup begins to establish its own territory. Maternal aggression, which begins at 9-10 weeks, increases gradually parallel to the pup's establishment of independent territory and probably triggers the dispersal from the maternal territory at an age of 11-12 week almost a month later than within the solitary genera of Bathyergidae (Bennett & Jarvis, 1988; Bennett *et al,* 1991).

One dispersal strategy to prevent inbreeding is for the male to establish its territory far from the maternal and female sibling

territories. It is possible that the higher maternal aggression exhibited toward the male pups encourages them to disperse earlier than female pups, as was shown in the present study, and also to establish their territories at a greater distance. In the present study, after the pups have established their territories adjacent to the maternal territory, the duration of continued interaction between mother and male pup was significantly longer than with female pup, although before dispersal, the duration of interaction with both was almost the same. These post-dispersal interactions are aggressive and might encourage the male to keep away from the territories of female relatives. Rado *et al,* (1992) found that males dig long, straight tunnels directly away from the maternal territory, and suggest that this method of male dispersal may prevent potential inbreeding and conforms to the strategy of many other mammals in which dispersal of males usually takes place at greater distances than that of females (Greenwood, 1980).

Although the adult blind mole rat is highly solitary and aggressive, maternal and sibling aggression is strongly reduced during the rearing period. Such a mechanism is essential for the pups to complete physical and behavioral development prior to dispersal. As long as the mother is in the vicinity of the pups, sibling aggression is suppressed, and fully emerges only immediately after separation from the mother. Under certain specific environmental and social conditions there appears to be some flexibility in the time of onset of aggression. For instance, during severe winter flooding, the pups remain restricted to the nest with their mother for a prolonged period. In this case, both the initiation of aggression and of dispersal are delayed (Zuri and Terkel, 1998).

Since aggression between adult mole rats often ends in the serious injury or death of one or both animals, and since the reproductive fitness of the mother increases as more pups survive, it seems reasonable for aggression between siblings to be inhibited as long as the pups remain within the social structure of the maternal tunnel system. However, once the young leave the maternal territory and establish and maintain their own territory, aggression becomes an essential behavior to deter intruders, including relatives. This argument supports the sharp increase in aggression exhibited by the pups immediately after separation from the maternal territory.

The first reported case of breeding the blind mole rat in captivity occurred between a mother and son which inhabited the same apparatus for several months (Gazit *et al*, 1996). It is our belief that the maintenance of the male pup with its mother in the original apparatus contributed to the successful reproduction in captivity by reducing the

animal's aggression. A similar success in reproduction of the solitary species *Georychus capensis* occurred when a mother mated with her male pup after a long period of cohabitation (Bennett & Jarvis, 1988).

The temporal correlation between the pups' establishment of separate nest and food store and their increased aggressive interactions might reflect the beginning of competition among pups over occupation of the adjacent tunnel system, nest materials and food items. Evidence for sibling competition has also been found in nature (Rado *et al,* 1992). During the summer, the dry soil becomes hard to excavate and a mole rat that has not completed digging its tunnel system and gathering food during the wet season will bear a severe energetic disadvantage. The mother, having spent most of her energy rearing the young, must at the same time also collect sufficient food items to ensure her own survival through the long summer. The significance of food storage, therefore, is crucial for the mother as well as for the young. The mother's tolerance of the female pup's removal of food from her store is mystifying as it decreases her own chances of survival. Although this behavior could provide a significant advantage to the young female, it is unclear why it is restricted exclusively to female pups, since to all appearances both female and male pups face the same obstacles of survival. These gender differences of behavior might be derived from the different dispersal pattern between males and females, under which the female pups establish their territories adjacent to the mother's territory, while the males establish their territories at a greater distance.

The advantage of the vibrational channel of communication used by the blind mole rat is that vibrations carry long distances through soil, making this mode of communication effective between animals in two separate territories (Rado *et al*, 1991; Zuri and Terkel, 1996); while the vocal channel of communication is used only as long as the mother and young stay in the same tunnel system. The young mole rat begins to be aware of the surrounding vibrations by jaw listening earlier than it starts to produce these vibrations itself. While still in the maternal territory, the ability to detect vibrations in the environment is vital in order to avoid intruders or predators. Producing vibrations at this stage is still not necessary for survival, but becomes significant later when digging new tunnels. In the present study we found that the young mole rat performs jaw listening and head drumming behaviors significantly more frequently in its own new tunnel than in the maternal territory. Since it depends on creating and receiving vibrations in order to sense its environment, jaw listening and head drumming behaviors are thus more necessary, and performed by the young more frequently, in its

new unfamiliar tunnels than in the well-known maternal territory. The use of drumming signals while still linked to the maternal tunnel enables the young to discern its neighbors' territories and direction of digging, as suggested by Rado *et al,* (1992), and later confirmed after monitoring mole rats in nature (Zuri and Terkel, 1996).

Use of the vibrational mode of communication by hind foot drumming for territorial advertisement has been described for solitary species of the family Bathyergidae *(Bathyergus suillus, B. janetta, Georychus capensis*), for the Rhyzomid *Tachyoryctes splendens* and for species of the Ctenomyidae and Geomyidae (Bennett and Jarvis, 1988; Bennett *et al,* 1991; Burda *et al*, 1990; Jarvis and Bennett, 1991; Narins *et al,* 1992). In most species, the use of seismic communication is initiated just prior to dispersal, except for species of the genus Bathyergus which first perform hind foot drumming 2-3 weeks after dispersal (Bennett *et al,* 1991), and thus probably do not use it to discern tunnel digging direction as in the blind mole rat.

In summary, the present study describes the gradual transition of the blind mole rat from altricial social infancy toward fully developed solitary maturity. Throughout the long developmental process the young channels its energy into growth and acquisition of skills such as digging, nest construction, food gathering, practice of vocal and seismic communication, and of aggressive behavior, all of which are vital for independent survival.

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