Blind mole-rats (Spalax ehrenbergi) are aggressive and solitary fossorial rodents, highly specialized to their environment. They use their lower incisors mainly to excavate their tunnel systems. We found that the lower incisors of the mole-rat grow significantly faster than the upper incisors. Upper and lower incisors of males grow significantly faster than incisors of females. Density of incisors of males was significantly higher than in females and in male laboratory rats (Rattus norvegicus). In both sexes of mole-rats, maxillary bone density at the root apex area of the incisor was significantly higher than the anterior area where incisors emerge from the bone and the same area densities in male laboratory rats. We suggest that the rapid growth rate and high density of incisors in mole-rats compared with male laboratory rats represent an adaptation to their digging life-style and compensate for the extensive incisor attrition resulting from the mechanical forces of digging. Intersexual differences in mole-rat incisor growth and incisor plus maxillary bone densities are in accordance with intersexual behavioral differences: males excavate wider and longer tunnels than females and are more aggressive. Because incisors of males are used more extensively in digging and fighting than those of females, we suggest that male mole-rats develop stronger incisors with a higher compensatory growth rate than females.

Key words: Spalax ehrenbergi, mole-rat, incisor, incisor adaptations

Blind mole-rats (Spalax ehrenbergi) are fossorial aggressive rodents that show morphological (Sanyal et al., 1990), physiological (Arieli and Ar, 1979; Nevo and Shkolnik, 1974), and behavioral (Nevo, 1991) adaptations to their underground environment. Zuri and Terkel (1996) showed that mole-rats continuously relocate their territories, in summer and winter, suggesting that they constantly dig and modify their tunnels. Like many other fossorial rodents (Genelly, 1965; Jarvis and Sale, 1971; Lessa, 1990), they use their incisors to shear the soil and their forepaws to dispose of it from the excavation site.

Male mole-rats invest more time and energy in digging than females, particularly at the beginning of the rainy (and breeding) season when they search for females by digging long straight tunnels (Rado et al., 1992). Heth et al. (1987) and Rado et al. (1987) suggested that mole-rats employ vibratory signals to enhance the likelihood of intersexual encounters during the breeding season and to deter aggressive neighbors. The effectiveness of vibratory signals in deterring invaders was confirmed in the field (Zuri and Terkel, 1996). Zuri et al. (1997) suggested that mole-rats also use territorial scent marking to delay intraspecific invasions. However, interactions between neighbors sometimes do occur and often end in the death or severe bite injury to one of the individuals and its expulsion from the tunnel system (Zuri, 1993; Zuri and Terkel, 1996). Although aggression was observed...
in both intrasexual and intersexual encounters (Nevo, 1969), it was more frequent between males (Nevo et al., 1986).

Intersexual differences in digging behavior led us to hypothesize that incisors of males are worn down more rapidly than those of females, and should have anatomical and physiological adaptations to compensate for wear and the external mechanical forces generated during digging. Compensation for incisor wear is important in males mainly because they dig more than females, but they are also the more aggressive sex and use their incisors to fight more than females.

Researchers have suggested that mechanical forces of digging are transmitted from tips of incisors backwards to molars in rodents that are specialized for digging with their teeth (Landry, 1957; Lessa, 1990). Therefore, we measured bone density at several locations in the maxilla, hypothesizing that bone density is higher near molars compared with frontal regions of the maxilla, to compensate for mechanical pressures in these regions.

We examined if the mole-rat had differential use and wear on upper and lower incisors during digging and intraspecific encounters. We also measured maxillary bone density, and upper and lower incisor growth rate and density, emphasizing interspecific and intersexual differences.

MATERIALS AND METHODS

Blind mole-rats are agricultural pests in Israel, and their capture is permitted by the government Natural Reserves Authority which monitors wildlife. Because mole-rats rarely breed in captivity (Gazit et al., 1996) and it is impossible to visually observe their behavior in nature, it is necessary to use wild-caught individuals for behavioral and anatomical studies. Our study was conducted according to the Guidelines of the Association for the Study of Animal Behaviour (Anonymous, 1996).

Seven male and seven female adult mole-rats belonging to the chromosomal form 2n  =  58 (Wahrman et al., 1969) were captured in non-cultivated areas that had been designated for road construction. Mole-rats were captured by exposing the most recently dug part of their tunnel, and trapping the animal with a hoe when it returned to close the exposed part of the tunnel (Zuri and Terek, 1996). To reduce stress, trapped animals were transferred to the laboratory immediately after capture and housed in standard rat cages. Although our capturing methods are the best way to trap this species alive, occasionally individuals do not survive the capture process. In these cases animals were transferred immediately to dry-ice containers and were used later to obtain morphological data to determine densities of skulls and incisors. These variables were also measured in three male laboratory rats (Rattus norvegicus). The rats were deeply anaesthetized with methyl ether to reduce stress and sacrificed by a cardiac injection of lethal dose of xylazine hydrochloride (Ketalar—Bayer Compan, Budapest, Hungary).

Mole-rats were housed individually in standard plastic cages (38 by 22 by 19.5 cm) with wire mesh tops and sawdust bedding and were fed carrots, apples, lettuce, and rat pellets (Koffolk Ltd., Tel-Aviv, Israel). Mole-rats were kept for 1 month at constant temperatures (25–27°C) under a 14L:10D light regime. Two mole-rats of each sex were transferred to experimental apparatus for observation of their incisor use during soil excavation and encountering sessions; the rest of the animals were used to determine growth rate of their incisors. Data on densities of skulls and incisors were provided from an additional 10 male and 6 female mole-rats that had died during capture.

After 10 days of acclimation to the test cage, we began observation of the use of incisors by the mole-rat during its excavation of a soil-plug. To determine incisor use during intraspecific encounters, two cages containing male-female pairs of mole-rats were connected for short periods, and the behavior of the animals was monitored. Preliminary observations on encountering mole-rats showed that both individuals push soil and sawdust bedding from their home cages toward the connecting arena as an avoidance barrier. The four mole-rats used for these observations encountered each other for a 5-min period only, and the observer was ready to separate them immediately in case of escalating aggression.

Burrowing behavior.—Two male and two fe-
male mole-rats were transferred to standard rat cages (38 by 33 by 16 cm), each connected to a 50-cm plexiglas tube, 6 cm in diameter. One side of each tube was blocked with two screws to prevent the escape of the test animal, and a parafilm seal prevented air flow into the tube. Following acclimation for 10 days, dry soil plugs were inserted into the plexiglas tubes after removing the screw-barriers, and the mole-rat's burrowing behavior was observed. The basic artificial soil plugs comprised soil mixed with water until a uniform viscosity was achieved. The mixture was placed in a 15-cm plexiglas tube, compressed to eliminate excess water, and dried at 120°C for 4 h for maximal dehydration.

Fighting behavior.—Observations were made on the same mole-rats previously observed digging, 5 days following the digging sessions. The dead-end plexiglas tubes of each pair of mole-rats were replaced with a single 60-cm tube that connected the two cages. Incisor use was monitored during 5-min intrasexual and intersexual encounters while the observer was ready to separate animals in case of escalation of aggression. One male pair and one female pair were observed during a single encounter. Forty-eight hours later, the behavior of one opposite-sex pair was monitored once. The encountering mole-rats were paired randomly.

Both excavating and fighting observations were videotaped with a JVC video camera (model VS-C 514 E) including time codes and were observed in real time, focusing on incisor use. Incisor use was reanalysed with a Panasonic AG 7300 (50 filts p.s.) after observations were completed.

Growth rates of mole-rat incisors were measured in nonanaesthesized individuals, because repeated anaesthesia could cause physiological harm and stress to mole-rats. We thus chose to hold them manually to mark their incisors and measure the relative notch position. Marking and measuring procedures were kept brief to minimize stress.

Incisor growth rate.—Growth rates of upper and lower incisors of adult mole-rats (5 of each sex) were measured for 1 month after their capture. Mole-rats were held in the hand and a fine transverse notch was made on the enamel of their incisors at the most ventral and most dorsal gum-lines of their upper and lower incisors, respectively. The notch was made with a Dremel (Moto-Tools, Model 258—Racine, Wisconsin) and steel disc. The distance of the groove from the gum lines was measured 6 days later. The length of time required to handle a mole-rat to make a notch or measure the notch location was 20–25 s.

Maxillary bone and incisor density (mm Al).—Data on maxillary bone and incisor radiographic image densities were collected from dead adult mole-rats (10 male and 6 female) and from three dead adult male laboratory rats. Analyses of densities of bones and incisors were based on x-ray analysis of hard tissues and comparison of the tissue image density to aluminum (Al) step-wedge density used as reference. The accuracy of this method was demonstrated by Plotnick et al. (1971) and Bodner et al. (1993).

To examine if there were significant differences between skull widths of male and female mole-rats and male laboratory rats, and therefore any effect of skull width on x-ray image density measurements, we measured skull interorbital width. In addition, we also removed zygomatic arches from all skulls before x-ray exposure.

Each maxilla and mandible were placed on EP-21 (Eastman Kodak Co., Rochester, NY) ANSI size-2 film with the buccal aspect of the jaw touching the film package. Maxillas and mandibles were exposed together with a pure (99.92%) Al step-wedge with 10 1.0-mm incremental steps from 1 to 10 mm. A Gendex 1000 x-ray machine (Gendex Company, Milwaukee, WI) was used for all exposures with a target-to-film distance of 45 cm and exposure time of 0.25 s at 65 kVp and 10 mA. The central ray was aligned perpendicular to the film in all exposures. The x-ray unit was checked for reproducible accuracy of exposure factor by the Department of Radiation Protection, Tel-Aviv University, using a Condenser-R-meter (Victoreen Inc., Carle Place, NY) and was found to be constant within a 5% limit.

Radiographs were processed at 20°C with an automatic processing machine (Durr Dental, D-7120, Durr Periomate, Bietigheim, Germany) with an 8-min cycle. Freshly mixed developer and fixer solutions were used to ensure proper processing. Image densities of maxillary bones were measured at four locations: 1. posterior part of the upper incisor, 2. near the upper incisor root apex location, and 3–4. in two locations where the incisor emerges from the maxillary bone. In addition, densities of upper and lower incisors were measured (Fig. 1). Optical
densities of bone and incisors were measured using the Ready Concept program (REDIK Ltd., New York). The optical density of the step-wedge 0 to 10 mm in each radiograph was measured, and a graph representing density versus millimeters of Al was plotted. Densities of bone and incisor were expressed in equivalent mm Al, thus providing an objective and repeatable parameter independent of exposure and developing conditions (Bodner et al., 1993; Plotnick et al., 1971). Data are represented as $X \pm SE$.

**RESULTS**

**Burrowing behavior.**—Male and female mole-rats approached soil plugs with open mouths and exposed teeth. After first contact with the soil, the animals sheared the soil with their lower incisors, moving their lower jaw forward and upward as in digging, but more rapidly. In five of six interactions, one or both animals retreated to their home cage for several seconds, pushing wood shavings with their heads in bulldozing movements, to make a physical barrier that separated them from their opponents. However, bites and attempted bites continued. In many cases, the lower incisors of one animal penetrated the wood-shaving barrier and clashed with the incisors of the opponent. If in a few cases, lower incisors also made contact with the gums of the opponent and scratched them. The upper incisors were used only occasionally during these encounters.

**Incisor growth rate.**—Lower incisors grew faster than the upper incisors (Wilcoxon's signed-ranks test, $P < 0.05$ for males and $P < 0.01$ for females). Upper and lower incisors of males grew faster than those of females (Mann-Whitney $U$-test = 0.00 $P < 0.01$ for upper and $P < 0.05$ for lower incisors; Fig. 2).

**Incisor density.**—Average interorbital width of male and female mole-rats and male laboratory rats was $6.9 \pm 0.1$ mm Al, $6.7 \pm 0.09$ and $6.9 \pm 0.4$, respectively, with no differences among groups (Kruskal-Wallis test, $P = 0.4$). Because there were no
differences in both variables between skulls, we expected that the nonsignificant differences in skull width would not affect image-density measurements.

Densities (mm Al) of upper and lower incisors of male mole-rats were higher than those of females (Mann-Whitney U-test, P < 0.05), and those of male laboratory rats (Mann-Whitney U-test, P < 0.05 for upper incisors and P < 0.01 for lower incisors). In female mole-rats, only the density of the upper incisors was higher than in male laboratory rats (Mann-Whitney U-test, P < 0.05). In male mole-rats, upper incisors were more dense compared with their own lower incisors (Wilcoxon’s signed-ranks test, P < 0.01, Table 1).

Maxillary bone density.—In male mole-rats, maxillary bone density (mm Al) at the root-apex regions of incisors was higher than in the anterior regions where incisors emerge from the maxillary bone (sites A and B compared with D. Fig. 1; Wilcoxon’s signed-rank test, P < 0.001 and P < 0.05, respectively). In female mole-rats, densities of sites A and B were higher than site D (Wilcoxon’s signed-ranks test, P < 0.01 for both comparisons), and in site B compared with C (Wilcoxon signed rank test, P < 0.05). There was no significant difference in bone density of male laboratory rats between anterior and posterior areas. Bone density of the laboratory rat was lower in regions A and D than in the same regions in both male and female mole-rats, respectively (Mann-Whitney U-test, P < 0.01 for all comparisons), and lower at regions B and C compared with the same regions, respectively, in male mole-rats (Mann-Whitney U-test, P < 0.05 for both comparisons; Table 2).

**DISCUSSION**

Most fossorial rodents are specialized to use claws or teeth for digging (Lessa, 1990, Lessa and Thaeler, 1989). In tooth-diggers, incisors suffer constant attrition, and the skull is exposed to mechanical forces of excavation. Lessa (1990) noted that although tooth-diggers mainly use their lower incisors to shear the soil, variations in procumbency and other structural features, to compensate for the mechanical forces during digging and incisor wear, appear to be in upper instead of lower incisors. It was suggested that the lower jaw movements, forward and upward, partially compensate for the mechanical pressures of digging, because pressure on the bone at the mandible that results from the digging activity is not concentrated on one location. However, during digging, the maxilla moves mainly at the vertical axis and pressure of digging is concentrated at the root site of the upper incisors, which are then procumbent for better angle of action against the soil. As procumbency of the upper incisors increases, rodents appear to be more specialized in tooth-digging, because more of the forces that are applied to the cutting tips are transmitted backwards to the upper molar teeth (Landry, 1957; Lessa, 1990). In specialized species, the roots of incisors lie posterior to the cheek teeth (Lessa, 1990). The blind mole-rat belongs to the tooth-diggers with
a "primitive" rostral structure because roots of its upper incisors are located anterior to the cheek teeth (Lessa, 1990; Topachevskii, 1976). Flynn et al. (1987) suggested that microstructure of incisor enamel in this species presents adaptations to soil types and that thickness itself is advantageous for digging.

We found growth rate of mole-rat incisors to be similar to that of the pocket gopher (Thomomys bottae), with the same pattern of faster growing lower (0.99 mm/day) compared to upper incisors (0.62 mm/day—Howard and Smith, 1952). Upper incisors of male mole-rats grew two to three times faster than those of laboratory rats (Rattus norvegicus—Marshall, 1921), guinea pigs (Cavia cobaya—Shadle et al., 1938), and North American porcupines (Erethizon dorsatum—Shadle et al., 1944).

Lower incisors of the mole-rat grew three to four times faster than those of the same animals. These interspecific differences are related to behavioral and ecological differences because mole-rats and pocket gophers are fossorial and constantly dig with their incisors, whereas the other rodents are not diggers. Although measurements of growth rates of incisors were conducted in the laboratory, we believe that they reflect the basic growth rate of incisors in the wild because measurements were conducted soon after the mole-rats were captured and they were provided with hard food material that resembled their food items in nature.

In both male and female mole-rats, lower incisors grew significantly faster than upper incisors and thus compensated for the greater attrition in lower incisors that resulted from digging activity. Upper and lower incisors of males grew faster than in females, and densities of upper and lower incisors of males were higher than in females. We suggest that intersexual differences in growth rates of mole-rat incisors and density result from behavioral differences between sexes. Because males dig wider and longer tunnels than females (Rado et al., 1992), their incisors become proportionally more worn and thus require greater compensation and grow faster and are stronger than those of females. It is interesting that upper incisors were significantly more dense than lower incisors only in male mole-rats. Lessa (1990) suggested that variations in root location and procumbency of incisors appear mostly in upper rather than lower jaws and are designed to overcome mechanical forces of digging. Lessa (1990) also proposed that lower incisors required less mechanical compensation for mechanical forces of digging because they were partially compensated by the movement of the lower jaw anteriorly during biting. Because only male mole-rats had significantly denser upper than lower incisors, we suggest that males are more adapted than females to continuous tooth-wear.

Maxillary bones of male and female mole-rats were significantly denser posteriorly, near the root apex of the incisor, compared with the anterior incisor area. These differences in bone density may have evolved as structural support for posterior areas of the maxillary bones, which are submitted to high mechanical forces that are transmitted back from the incisor tips while digging (Landry, 1957; Lessa, 1990). Although not significantly more dense than posterior areas, the maxillary bone density in region C (Fig. 1) in the male mole-rats was relatively high. The cortical bone in this area is very narrow and comprised mostly from two plates of cortical bone with almost no cancellous bone. Because males dig more than females, new bone production and therefore high bone density in maxillary region C is evident mainly in males and not in females. Maxillary bone density in male laboratory rats was significantly lower at all sites compared with the same sites in mole-rats. Because laboratory rats do not dig as much as mole-rats, their jaws are not exposed to extensive mechanical digging forces, and thus they have evolved a less massive upper jaw. We also found that incisors of male laboratory rats were less dense than those of mole-rats.
Parallel evidence for correlation between biting forces and bone-plus-teeth strength also has been found in carnivores, suggesting that tooth strength is correlated with killing behavior; (i.e., as bite forces increase due to large oblique or mediolateral bending stresses, canine teeth are larger and stronger—Van Valkenburgh and Ruff, 1987).

Our finding of faster growth rate in lower incisors of mole-rats appears to be related to their primary use for digging; paradoxically however, lower incisors are less dense than upper ones, but because they are subjected to more extensive wear, they are compensated by a faster growth rate than upper incisors.

In addition to using incisors in feeding and digging, mole-rats use them as their only weapon during intraspecific interactions. Teeth also are used as the major intraspecific weapon in other fossorial (Eileen and Baker, 1974; Howard and Smith, 1952) and non-fossorial rodents (Ghosh et al., 1983) and larger mammals. Male narwhals (Monodon monoceros) use their elongated tusk during intrasexual fights (Gerson and Hickie, 1985; Silverman and Dunbar, 1980), and the upper canine teeth of the walrus (Odobenus rosmarus) develop into great tusks that provide the sole, and deadly, weapon during intraspecific and mostly intrasexual interactions (Macdonald, 1984). Large lower canines of the adult male hippopotamus (Hippopotamus amphibius) are the chief weapon (Nowak, 1991). Lups and Roper (1988) suggested that intraspecific competition in the European badger (Meles meles) is correlated with sexual dimorphism in canine size, with males having the strongest and largest anterior teeth because they fight more than females. Adapting to life underground, mole-rats have evolved for specialized incisor-digging, as indicated by fast growing incisors and stronger skulls plus incisors compared with non-fossorial rodents. Intersexual behavioral differences, with males digging and fighting more than females, may explain their stronger and fast-growing lower incisors, which are their only weapon.

The extensive use of incisors sometimes may result in broken teeth and even the death of the animal; a domestic hog starved and died after its incisors broke due to high mechanical forces exerted by eating turnips (Orr, 1985). Extensive wear in domestic sheep incisors, as a consequence of foraging on winter grass, can cause infections in the pulp cavities (Thurley, 1985). Continuous observations on three mole-rats with broken upper incisors revealed a progressive decrease in body weight; two of these animals lost both upper incisors and within several days their lower incisors overgrew and caused eating difficulties. Furthermore, to prevent penetration of lower incisors into skulls in these animals, it was necessary to cut them every 4 days. Because mole-rats are highly aggressive, and sometimes invade territories and fight neighboring individuals, we suggest that excessive incisor wear or breakage may be detrimental during intraspecific interactions and could result in the death of the unprotected toothless individual.

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