An Ethogram for the Naked Mole-Rat: Nonvocal Behaviors

Eileen A. Lacey, Richard D. Alexander, Stanton H. Braude, Paul W. Sherman, and Jennifer U. M. Jarvis

Ethograms are species-specific catalogs of behavior that describe an animal’s actions to individuals not familiar with that organism. Ethograms also provide standardized labels for behaviors that can be used by different investigators, thereby increasing the consistency and repeatability of behavioral studies. Ideally, biologists would like to determine the reproductive significance of each aspect of an organism’s behavior, since natural selection acts to shape behavior through differences in reproductive success. However, the reproductive consequences of individual behaviors are only rarely understood. As a result, ethologists are faced with a choice: they can characterize behaviors in ways that imply function even when reproductive significance has not been demonstrated, or they can characterize behaviors in ways that are primarily descriptive (but that provide little information about function) even when some evidence of adaptive significance is available.

Here we present an ethogram for the naked mole-rat. Nonvocal behaviors are described in this chapter; vocal behaviors are addressed in the next. Although some readers may find these chapters less theoretically stimulating than others, we note that while the unusual social organization of *Heterocephalus glaber* has been well documented (e.g., Jarvis 1981; this volume), the behavioral repertoire of this species has not been formally characterized. The most appropriate place for such a characterization is in this volume, particularly because many subsequent chapters rely on the terminology and descriptions of behaviors that are presented here.

In constructing this ethogram, we compromised between the functional and descriptive approaches outlined above; whereas the labels and explanatory text used to characterize each behavior are descriptive and lack functional connotation, the order in which the behaviors are presented is intended to suggest functional similarities between activities. Specifically, the 72 nonvocal behaviors of naked mole-rats described here have been grouped into 17 categories based on presumed functional similarity; these categories are intended to serve as hypotheses regarding the adaptive significance of the behaviors described. As additional data regarding reproductive significance become available and
the presumed adaptive functions of behaviors become clearer, the behaviors in question can simply be moved from one category to another; the labels and explanatory text associated with these activities need not be altered. We believe that our approach represents the most effective means of presenting adaptive hypotheses without compromising the utility of the descriptive labels and explanations used to characterize behaviors.

Methods

The following ethogram was developed from observations of naked mole-rat behavior conducted by the authors. An initial list of behaviors was compiled during discussions at Ann Arbor, Michigan in July 1985 (see the Preface). Quantitative data regarding specific behaviors were later obtained from observations of colonies housed in translucent (acrylic plastic [i.e., plexiglass] or glass) tunnel systems in laboratories at Cornell University (n = 5 colonies), the University of Michigan (n = 3 colonies), and the University of Cape Town (n > 20 colonies). The methods used to house and maintain these colonies are described by Jarvis in the Appendix.

Each behavior has been given a descriptive, mnemonic label; for behaviors not identifiable by label alone, a more detailed description of the actions comprising that behavior has been developed. Both labels and associated explanations are descriptive. Photographs of selected behaviors are included (see also Pennisi 1986), along with line drawings to highlight particular details. Whenever possible, the subset of colony members performing a particular behavior and the context in which the behavior occurs have also been characterized. To suggest adaptive functions for specific activities, behaviors have been grouped into categories based on presumed functional similarities. Behaviors were categorized on the basis of (1) evidence of adaptive significance and (2) apparent functional congruence with similar behaviors in other species. This ethogram is intended to serve both as a guide to the behaviors discussed elsewhere in this volume and as a reference for future studies of naked mole-rat behavior.

Descriptions of Behaviors

GROOMING

Naked mole-rats exhibit the following behaviors associated with grooming their own bodies (i.e., autogrooming):

1. Cleaning the forefeet or hind feet with the incisors
2. Cleaning the incisors with the forefeet
3. Wiping the face and muzzle with both forefeet
4. Scratching the flank, underarm, mouth, or head regions with the hind foot (fig. 8-1)
5. Grooming the tail with the teeth or forefeet
6. Grooming the genitals with the tongue or incisors
7. Honing the incisors

When honing the incisors, mole-rats rub together the ends of the incisors, typically with the bottom incisors extending beyond the top ones such that grinding occurs on the inner surface of the lower teeth and the outer surface of the upper teeth. Incisor honing often occurs when the animals are reclining (below).

Autogrooming occurs at a low but consistent frequency; 1.3% ± 0.1% of data points per individual collected during scan sampling consisted of observations of autogrooming (10-min scan intervals; ≥ 125 scans per animal; n = 65 animals in three Cornell colonies). In contrast, allogrooming is almost never observed among adult naked mole-rats. Although adults do groom pups (e.g., licking or nibbling pups, see "Neonate Tending," p. 231), similar behaviors are not observed among adults.

Ectoparasites of Heterocephalus glaber include the subcutaneous hypodermitid mite Acoylyopus canestrini (Parona 1895), the chigger Euschongastia bottegi (Parona 1895), and an undescribed species of mite in the genus Androlaelaps (B. M. O'Connor, pers. comm.; collected by S.H.B.). However, the virtual absence of allogrooming in H. glaber adults suggests that (1) these parasites are not common in the laboratory, (2) they do not cause significant irritation to the animals, or (3) individuals are able to deal with their own parasites more effectively than another animal could. Clearly, allogrooming in H. glaber has not developed the complex secondary social functions that it has in other highly social mammals, most notably primates such as bonnet macaques (Macaca radiata, Silk 1982) and savannah baboons (Papio cynocephalus, Saunders 1988; see also reviews in Sparks 1967; Seyfarth 1977, 1983).

**Fig. 8-1.** A naked mole-rat scratching its face with a hind foot. Scratching occurs either as a part of autogrooming or immediately following urination. Scratching that occurs in the latter context is much more vigorous and exaggerated than scratching that is not associated with urination.
Fig. 8-2. A group of naked mole-rats reclining in a nest box. Reclining is characterized by the relaxed position of the animals, as well as by the absence of any locomotor activity. The mole-rats may recline alone but are typically observed reclining in physical contact with other colony members (e.g., in the nest).

RESTING

Resting behaviors are characterized by a lack of motor activity. Although it is difficult to demonstrate that an animal is actually resting or sleeping, we can say that it is not engaged in any other identifiable activity. Behaviors categorized as resting are:

1. Yawning
2. Dozing
3. Reclining

When dozing an animal stands motionless with its head drooped, giving the impression that it is asleep on its feet. Dozing is typically observed in the tunnels, frequently at sites where lamps provide a localized source of heat. Animals may doze singly or in small groups of two to four.

Also called huddling (e.g., Withers and Jarvis 1980; Jarvis 1981), reclining occurs when an animal lies on its side, back, or stomach with its eyes closed, apparently asleep; often the limbs twitch slightly. Mole-rats may recline singly or in groups; animals reclining in groups are in physical contact with one another, often with individuals lying on top of, as well as beside others (fig. 8-2).

Reclining represents a substantial portion of an individual's daily activity. For nonbreeding animals (*n* = 56) in three Cornell colonies, 56%–61% of data...
Plate 8-1. Top, A group of naked mole-rats reclining (or huddling) in the colony’s nest, the breeding female (nipples visible) is in the center of the pile, and two 2-3-day-old pups are in the foreground. Bottom, A close-up of a similar nest huddle showing how tightly the mole-rats pack themselves. Photos: J.U.M. Jarvis, R. A. Mendez.
points per individual collected during scan sampling consisted of observations of reclining (10-min scan interval; \( n \approx 125 \) scans/animal). Breeding males in these colonies \( (n = 5) \) behaved similarly; 58%–65% of data points for these animals consisted of observations of reclining. In contrast, breeding females in these colonies \( (n = 4) \) were observed reclining during only 34%–46% of data points from activity scans (see also Reeve and Sherman, chap. 11).

Although naked mole-rats may recline singly, individuals are most frequently observed reclining in large groups \( (>10 \text{ animals}) \) in the colony’s nest box (plate 8-1). It was our strong impression (confirmed by Jarvis, chap. 13) that the tendency of individuals to recline in groups in the nest increased shortly before a litter of pups was born into a colony; this suggests that reclining in groups may have either thermoregulatory or antipredator significance. Yawning is depicted in plate 2-1 (p. 57).

**Thermoregulation**

The thermoregulatory physiology of naked mole-rats has been studied by numerous investigators (e.g., Johansen et al. 1976; Mustafa et al. 1981; see Jarvis and Bennett, chap. 3). Naked mole-rats are unusual in that they are virtually hairless and essentially ectothermic. In captivity, the body temperatures of individuals vary directly with ambient temperature (McNab 1966). In the field, however, naked mole-rats are thought to be functionally homeothermic because of the thermal stability of their subterranean environment (Jarvis 1978) and behavioral mechanisms of thermoregulation (Withers and Jarvis 1980). In the laboratory, the following behaviors appear to be associated with thermoregulation:

1. Crouching
2. Shivering
3. Basking

A crouching animal stands in a hunched posture, in physical contact with other colony members. Individuals often shiver while crouching. Crouching differs from reclining in that animals are standing, rather than lying down. Crouching differs from dozing in that dozing animals are relaxed, whereas crouching mole-rats assume a hunched posture. Reclining typically occurs in nest boxes, but crouching and dozing are most commonly observed in the tunnels.

Shivering is a very rapid shaking or quivering of the body and extremities. An animal stands in a hunched posture, with the extremities held under the body. Unlike the jerking motion associated with the loud chirp vocalization (Pepper et al., chap. 9), shivering is characterized by individual convulsions of small amplitude, too rapid to be distinguishable from one another.

A basking animal stands with its back or side against a tunnel wall, typically
under electric lamps that provide localized heat sources. Basking differs from
dozing in that the animal's head does not droop, but, along with the body, is
pressed tightly against the warm tunnel wall.

Naked mole-rats in our lab colonies appeared to respond behaviorally to
changes in ambient temperature. Specifically, colony members spent more
time crouching when the ambient temperature was low (e.g., < 23°C; also
Withers and Jarvis 1980). Furthermore, the locations at which basking typi-
cally occurred corresponded to the locations of electric lamps, and altering the
locations of these lamps could induce colonies to switch nest boxes and bask-
ing sites.

Individuals were also observed to shiver when the ambient temperature was
low. In addition, shivering was observed in two contexts not necessarily asso-
ciated with thermoregulation: shivering by pregnant females while crouching
or reclining in the nest, and shivering by injured or diseased animals. Shivering
in these contexts may reflect physiological stress in addition to attempts to
thermoregulate.

Feeding

In the field, naked mole-rats feed on large subterranean tubers (e.g., Pyrena-
cantha kaurabassana; Brett, chap. 5). The animals tunnel through the soil to
reach these tubers and then apparently consume them there by gradually hol-
loowing out the tuberous portion of the plant (plate 8-2). The animals also feed
on smaller corms and roots (e.g., the legume Macrotyloma maranguense;
Brett, chap. 5) that are apparently transported to the nest for consumption. Five
feeding behaviors have been observed in the laboratory:

1. Brushing food
2. Licking food with the tongue
3. Gnawing
4. Nibbling
5. Chewing

Brushing food involves rapidly moving the forefeet up and down along
the sides of a food item that is held in the incisors. Brushing is typically ob-
served before an animal begins feeding on small wet or dirt-covered food
items; brushing is not observed while animals are gnawing on large food
items.

When gnawing, an animal stands with its legs braced against the sides or
floor of a tunnel. The incisors are closed across the surface of a large food item
(e.g., a tuber), thereby scraping off small bits of food (fig. 8-3; plate 8-2, top).
A nibbling animal holds a food item with both forepaws (often while reclin-
ing) and consumes small portions of food using the tongue and incisors (fig.
8-4).
Plate 8-2. *Top,* A naked mole-rat gnawing on a subterranean tuber. *Bottom,* A mole-rat has gnawed through the tuber. The animals consume large tubers by removing small pieces; sometimes these are carried back to the nest. Photos: R. A. Mendez.
Fig. 8-3. A naked mole-rat gnawing at a large tuber. Gnawing is characteristic of animals feeding on large, hard food items. The legs are braced against the tunnel walls, and the incisors are used to scrape small slivers of food from the tuber.

Fig. 8-4. A naked mole-rat nibbling on a piece of food. Nibbling is characteristic of animals feeding on small or soft food items. The food item is held between the forepaws and consumed using the tongue and incisors.

The type of feeding behavior observed appears to depend on the size and consistency of the food item being consumed. Gnawing typically occurs when an animal attempts to consume a large, hard, unmovable food item, whereas nibbling occurs when animals consume small or soft (e.g., bananas) pieces of food that can be held with the forefeet. In captivity, feeding behaviors are observed in all portions of the tunnel system, although these behaviors are most common at the site where food is introduced and in the nest box. The types of food items consumed by laboratory colonies are discussed by Jarvis in the Appendix. Behaviors associated with transporting food items through the tunnel system are discussed below.

**Elimination**

Naked mole-rats usually urinate and defecate in specific areas of the tunnel system, typically in dead-end tunnels or in boxes with only a single tunnel access ("toilet" boxes). All colony members appear to use the same toilet area or areas. Elimination behaviors include:
Fig. 8-5. A naked mole-rat urinating. The ano-genital area is extended toward the substrate, with the tail held above the body.

1. Defecating
2. Urinating (fig. 8-5)
3. Urinating with crotch dragging
4. Urinating with scratching
5. Wallowing

Defecating mole-rats expel two types of feces: moist, soft, light-colored feces that are often immediately reingested by the defecating animal (or a colony mate) and that may function as caecotrophs, and dry, hard, dark-colored feces that are not consumed directly (but may occasionally be retrieved from toilet areas and eaten). Animals excreting the first type of feces assume the doubled-up posture typical of autocrophagy (see below); in contrast, animals excreting the second type of feces stand in a hunched posture with the tail raised away from the substrate.

In urinating with crotch dragging, an animal urinates with the hind legs splayed and the ano-genital area extended toward the substrate (fig. 8-5). Immediately following urination, the animal drags its ano-genital area along the floor of the toilet area.

In urinating with scratching, an animal scratches its head, shoulders, or open mouth with a hind foot immediately after urinating (as in fig. 8-1). This type of scratching is much more vigorous and exaggerated than the scratching associated with grooming and occurs exclusively after urination while the animal is in the toilet box or in the tunnel leading to it. Scratching associated with urination may be either preceded or followed by wallowing.

A wallowing animal rubs its shoulders or flanks against the bottom or sides of the toilet box or a nearby tunnel immediately after urinating or defecating; sometimes a wallowing animal rolls onto its back (plate 8-3). Wallowing often immediately precedes or follows scratching of the head and shoulders. Wallowing typically occurs in the toilet area; the occurrence of wallowing may be related to the wetness of the substrate in the toilet (O'Riain, pers. comm.).

Elimination behaviors appear to fall into two categories: those associated only with the physiological need to excrete wastes (e.g., 1 and 2), and those
that involve more elaborate behavior patterns with apparent social functions (e.g., 3–5). The urine of naked mole-rats may contain semiochemicals which function in nest-mate recognition. Wallowing and scratching are two ways that colony members can cover themselves with urine and feces, thereby acquiring or reinforcing their own distinctive colony odor.

COPROPHAGY

Adult naked mole-rats consume both their own feces and the feces of other colony members. Three behaviors are associated with coprophagy:

1. Autocoprophagy
2. Allocoprophagy
3. Begging

In *autocoprophagy*, an animal consumes its own feces, typically while doubled over so that it is sitting on its hindquarters with its mouth in contact with its anus (fig. 8-6).

Allocoprophagy is the consumption of the feces of another colony member. Allocoprophagy is typically preceded by begging for feces.

A *begging* animal uses its muzzle to nudge and tug at the anal area of a colony mate. The begging animal gives a special vocalization (Pepper et al.,
Fig. 8-6. Autocoprophagy. Naked mole-rats consume their own feces by doubling over so that the mouth is in contact with the ano-genital area.

Fig. 8-7. A naked mole-rat pup begging for feces from an adult colony mate. The pup nudges and tugs at the ano-genital area of the adult with its muzzle. The animal providing feces either lies on its back or assumes a doubled over posture with its muzzle near its ano-genital area.

chap. 9). The individual providing feces either lies on its back or assumes the doubled-up posture typical of autocoprophagy (fig. 8-7).

Coprophagy is an essential part of the nutrition of some lagomorphs (see Thacker and Brandt 1955), rodents (see Barnes et al. 1963), and termites (Waller and La Fage 1987). It seems likely that naked mole-rats also obtain nutrients by consuming feces (their own and those of colony mates). Pups beg for feces as they approach weaning (plate 8-4), and feces appear to provide a transitional source of food as pups cease to nurse and begin to consume solid food. Consumption of feces may also provide pups with endosymbiotic gut flora (Porter 1957), as in many termites (La Fage and Nutting 1978). In lab colonies studied by Jarvis (chap. 13), only nonbreeders provided feces to pups.

Among adults, begging is apparently exhibited only by the breeding female. Of 21 incidents of begging by adults observed at Cornell, all were by breeding
Plate 8-4. A naked mole-rat pup begging feces from a nonbreeding adult (sitting up, doubled over), the pup in this photo is about 4-wk old and nearly weaned. Photo: J.U.M. Jarvis.

females. In 14 (66%) of these incidents, begging was directed toward a breeding male. Thus, although breeding females did beg and receive feces from nonbreeding colony members, allocoprophagy among adults occurred primarily between two breeding animals.

Locomotion

Naked mole-rats have exhibited several forms of locomotor activities in the artificial burrow systems in our laboratories:

1. Walking (forward or backward)
2. Running (forward or backward)
3. Splayed walking
4. Crouch advancing
5. Darting
6. Swimming
7. Passing
8. Turning

In splayed walking, an animal walks with its legs held out to the sides of its body (resembling the stance of a salamander) and its trunk held close to the substrate.
Fig. 8-8. Two naked mole-rats passing each other in a tunnel. One animal, usually the smaller one, crouches against the bottom of the tunnel (top) and the other (usually larger) individual crawls over the crouching animal (bottom). Mole-rats can also pass side by side while moving through a tunnel.

Fig. 8-9. A naked mole-rat reversing its direction of locomotion by using a T-shaped tunnel junction to execute a three-point turn. The animal first passes the T junction (a), then back into the branch of the junction that runs perpendicular to the direction of motion (b). The mole-rat then turns and resumes locomotion (but in the opposite direction) down the stretch of tunnel from which it had initially come (c).
Table 8-1
The Relative Frequencies of Occurrence of the Four Most Commonly Observed Types of Locomotion

<table>
<thead>
<tr>
<th>Type of Locomotion</th>
<th>Times Observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Walking forward</td>
<td>32</td>
</tr>
<tr>
<td>Walking backward</td>
<td>15</td>
</tr>
<tr>
<td>Running forward</td>
<td>104</td>
</tr>
<tr>
<td>Running backward</td>
<td>38</td>
</tr>
<tr>
<td>Total</td>
<td>189</td>
</tr>
</tbody>
</table>

Note: Data are from a random sample of 189 instances in which non-breeding animals moved a distance of 20 cm or more. A total of 42 animals in two colonies were observed at Cornell during 1986; the movements of each animal were sampled three to eight times.

In the behavior called *crouch advancing*, an animal moves forward a few steps with its legs bent and its body held close to the substrate; the animal pauses, and then moves forward again. This form of locomotion is most frequently observed following some type of colony disturbance (e.g., opening the tunnel system; see "Alarm Reactions," p. 240).

A *darting* animal very rapidly moves a short distance (one to two body lengths) forward or backward.

Naked mole-rats do have some *swimming* ability. W. J. Hamilton, Jr. (1928) and Hickman (1983) reported that naked mole-rats are able to keep themselves afloat for periods of up to 2 h by simultaneously dog-paddling with the hind feet and sculling with the tail.

Two animals *passing* one another while moving through the tunnel system may pass side by side, or, more commonly, one over the other (fig. 8-8). Individuals may pass one another while moving either forward or backward.

*Turning* animals can reverse the direction of locomotion by completing a forward somersault followed by a 180° twist, such that the ventral portion of the body faces the substrate. Alternatively, individuals can reverse direction by completing a three-point turn in which the animal passes a T-shaped junction in the tunnel system (in nature, a small outpocketing), backs into the branch of the T perpendicular to the direction of movement, turns 90°, and resumes locomotion (but in the opposite direction) back down the stretch of tunnel that it came from (fig. 8-9).

Naked mole-rats appear to move forward or backward with equal rapidity. In a randomly chosen sample of 189 instances of locomotion (data from two colonies at Cornell, n = 42 animals observed), 75% were observations of running, and 25% were of walking (table 8-1). The animals moved most rapidly when traversing long (3–5 m), straight stretches of tunnel.
The type of locomotion exhibited by naked mole-rats changes if the animals are removed from the tunnel system. When they are placed in an open, flat area (e.g., a table top), locomotion consists primarily of splayed walking. The animals exhibit no apparent perception of "edges;" locomotion does not slow or otherwise visibly change as the animals approach drop-offs. Furthermore, the mole-rats will repeatedly fall off such edges, giving no indication that they learn to detect and respond to edges.

When mole-rats encounter one another in the tunnel system, one individual may pass over the other or both may pass side by side. It was our impression that passing side by side occurred most frequently when similar-sized small mole-rats encountered one another. Among members of three Cornell colonies (n = 65 animals), the tendency to pass over other individuals correlated significantly and positively with body weight (all r > 0.56, all p < 0.01). Although breeding females were among the largest individuals in the colonies, they passed over colony mates no more frequently than predicted on the basis of body size. Thus, it may simply be easier for a small mole-rat to squat and let a large one step over it than vice versa.

Orientation

The sensory capabilities of naked mole-rats have not been quantitatively examined. However, the animals' morphology, in particular the minute size of the eyes, suggests that vision is a less important sensory modality than touch, olfaction (see Tucker 1981), or hearing (Pepper et al., chap. 9). Several orientation behaviors have been observed in our laboratory colonies:

1. Sniffing
2. Head pressing
3. Exit darting
4. Tail sweeping

During head pressing, an animal stands motionless with the top of its head pressed against the ceiling of a tunnel.

In exit darting, an animal in a nest box darts (see "Locomotion," above) forward until its nose contacts the sides of the nest box. The animal then darts backward several steps before repeating the forward motion. This pattern is repeated several times until the animal arrives at a tunnel opening leading out of the nest box.

An animal engaged in tail sweeping moves its tail from side to side (the tail often contacts the tunnel walls) while walking, running, or sweeping (e.g., nesting material; below); tail sweeping is especially pronounced when animals are moving backward through their burrow systems.

Orientation behaviors are particularly apparent when a colony is disturbed (e.g., by the introduction of a new tunnel or an unfamiliar conspecific), or
when a colony is hungry and numerous individuals are searching for food. Individuals encountering a foreign mole-rat or a novel object alternately approach and retreat from the area, exhibiting both the crouch advance and frequent head presses. The animals also sniff intently at any newly introduced object, typically approaching it, sniffing briefly, and then retreating rapidly (one to two body lengths) before advancing again. The vibrissae and the stiff hairs on the tail are also likely used to obtain (tactile) information concerning the environment (Hill et al. 1957; Tucker 1981).

Naked mole-rats appear to learn tunnel configurations, as indicated by an increase in the speed of backward and forward locomotion once the animals have made several passes through a novel tunnel configuration and frequent navigational mistakes (bumping into walls) following changes in tunnel system configuration. In addition, the animals often walk through the tunnel system with their eyes apparently closed. Interestingly, in the field, mole-rat colonies whose tunnel systems have been experimentally bisected are able to orient the direction of tunnel excavation so as to exactly reconnect the severed tunnels (Brett 1986, chap. 5); how the two halves of a colony orient toward each other is unknown.

**Transport**

In the laboratory, naked mole-rats transport a variety of materials (e.g., pieces of food, nesting material, chunks of dirt, small stones; see plates 10-2, 10-3) through the tunnel system. In the field, both corms and the husks of bulbs are found in nests, indicating that these items are transported through the burrows (Brett, chap. 5). In both the field and lab, the tunnels are free of food remnants and debris, suggesting that the burrows are being cleaned frequently. Four methods of transport have been noted:

1. Mouth carrying
2. Dragging
3. Sweeping
4. Backward kicking

A mole-rat engaged in **mouth carrying** holds an item between the incisors and lifts it off the tunnel floor. Items may be carried in this way while the animal is moving either forward or backward (fig. 8-10; plate 8-5).

In **dragging**, an item is held with the incisors and dragged along the tunnel floor, usually while the animal is moving backward through the tunnel system.

A **sweeping** mole-rat kicks loose items (e.g., sand, dirt, wood shavings) behind itself while moving backward through a tunnel. The hind feet are rotated outward and the legs are synchronously lifted and kicked backward several times as the animal balances on its forelegs. The animal then moves a step or two backward before repeating this kicking motion.
Fig. 8-10. A naked mole-rat carrying a piece of food in its mouth. The piece of food is held between the incisors and lifted off the substrate. This method of transport is typically associated with small objects; large or heavy items are dragged.

Plate 8-5. A nonbreeding naked mole-rat carrying a piece of food it has just excised from a large tuber. Photo: R. A. Mendez.

Backward kicking occurs when the back legs are synchronously lifted and kicked upward, propelling material above and behind the animal (fig. 8-11). In contrast to sweeping, material is moved vertically (i.e., upward) as well as horizontally, and the animal does not move backward between successive kicks.

Whether objects are carried or dragged appears to depend on their size: smaller items (e.g., bits of food) are usually carried (plate 8-5), whereas larger items (e.g., rocks) are typically dragged. Items that are apparently either too small or too numerous (e.g., wood shavings used as nesting material) to be easily picked up with the incisors are swept through the tunnels. Although all
nonbreeding colony members transport food, nesting material, and dirt through the tunnel system, transport behaviors are most commonly exhibited by smaller nonbreeders (Lacey and Sherman, chap. 10; Jarvis et al., chap. 12; Faulkes et al., chap. 14).

In the field, the backward kick is used to expel loose soil from the tunnel system (Jarvis and Sale 1971; Brett, chap. 5; Braude, chap. 6). In the laboratory, the backward kick is often used to move loose dirt into an empty nest box.

**DIGGING**

Naked mole-rats are fossorial, and digging clearly represents an important part of the animals' behavioral repertoire. In the field, *H. glaber* colonies are most easily found by locating the molehills (Brett, chap. 5) or "volcanos" (Braude, chap. 6) formed as the animals eject soil loosened by digging from their burrow systems. The digging behavior of naked mole-rats is a cooperative activity in which chains of individuals help excavate dirt and transport loose soil to burrow entrances (Jarvis and Sale 1971; see also Jarvis et al., chap. 12; Jarvis 1984). In the laboratory, the animals readily dig when provided with an appro-
appropriate substrate such as dirt (Lacey and Sherman, chap. 10; Jarvis, chap. 13) or cork (Pepper et al., chap. 9). Three digging behaviors have been observed in the lab:

1. Gnawing  
2. Backshoveling  
3. Foreleg digging

In *gnawing*, the incisors are scraped along a dirt face, loosening chunks of soil (plate 8-6). This is the predominant mode of excavation, especially when animals are working on hard surfaces.

*Backshoveling* means that the forelegs are synchronously lifted, moved forward and down onto a pile of dirt, and then moved backward under the body, propelling the dirt underneath and slightly behind the animal.

*Foreleg digging* occurs when one foreleg is brought forward and the foot is scraped along a dirt face, removing small pieces of dirt; the foreleg is then returned to a position under the body. The action is usually repeated rapidly using alternate forelegs. Foreleg digging and gnawing often occur in succession; an animal first gnaws at the earthen face for 15–30 s, then moves loosened dirt out of the way using the foreleg dig and backshovel.

Digging is one of the most important behaviors of naked mole-rats. Because observing the details of tunnel excavation in the field is impossible, we must
rely on inferences from laboratory observations. In captivity, all nonbreeding animals perform the three digging behaviors described above. However, it is currently somewhat unclear which colony members participate most frequently in these activities. Both positive (Braude 1983; Lacey and Sherman, chap. 10) and negative (Jarvis et al., chapt. 12) relationships between body weight and gnawing and digging frequency have been reported. The reader is referred to the relevant data and discussions in chapters 5, 10, and 12 of this volume.

**Mating**

The most distinctive feature of the mating system of naked mole-rats is that sexual activity is usually limited to a single female and one to three males per colony (Lacey and Sherman, chap. 10; Jarvis, chap. 13). There are three mating behaviors:

1. Backing
2. Mounting
3. Copulating

In **backing** behavior, the breeding female backs up to a male, exhibiting a lordosis-like posture that exposes her genitalia. During backing, the breeding female often gives a distinctive trilling vocalization (Pepper et al., chap. 9).

**Mounting** the breeding female from behind, the male typically braces his front legs against the sides of the tunnel system. He exhibits a pedaling motion of the hind legs as he attempts to bring his genitals into contact with those of the female (fig. 8-12).

**Copulating** is defined by contact between the genitalia of the male and female. Pelvic thrusting by the male is observed just before and during copulation. Ejaculation is not obvious. Copulations last less than 15 s, after which the male dismounts.

Female naked mole-rats exhibit behavioral estrus for 24 h or less. During this period, breeding animals remain in close proximity and move frequently around the tunnel system. Numerous mounting attempts occur but do not result in copulations. Aggression among breeding males does not occur during the breeding female’s estrus, although aggression may be observed several days before mating (Lacey and Sherman, chap. 10; Jarvis, chap. 13).

Copulations and attempted copulations appear to occur whenever the estrous female encounters a breeding male in the tunnel system. Of 38 copulations observed at Cornell, 26 (68%) were initiated when the breeding female approached and backed up to a breeding male. The remaining 12 copulations (32%) were initiated when a breeding male approached, nuzzled, and mounted the breeding female. Mounting by males was also frequently observed during late pregnancy; the function of these mountings is unknown. Mounting and
other sexual behaviors are not exhibited by nonbreeding colony members. Mating behavior is described in greater detail in Chapter 13.

Reproductive behavior in laboratory colonies is often associated with a fourth behavior, ano-genital nuzzling. Because ano-genital nuzzling between breeding animals is observed during all phases of the female's reproductive cycle and because ano-genital nuzzling is occasionally observed between nonbreeding animals (Jarvis, chap. 13), this activity has been categorized as an interactive behavior (see p. 235) rather than a mating behavior.

**BIRTHING**

Birthing consists of a single behavior, *parturition*. A female that is about to give birth becomes very active, running through the tunnel system with frequent pauses to nudge or lick her genital area. She may also autogroom intensely during this period. Pups are typically born head first, and the head of a pup may be seen protruding from the female's vagina as she moves through the tunnel system. As the pup is finally expelled from the female's reproductive tract, the female often doubles over so that she is sitting on her hindquarters, with her muzzle in close proximity to her genital region (e.g., see figs. 8-6, 8-7); the female sometimes pulls at the pup (or afterbirth) with her incisors, apparently helping to remove the pup from her reproductive tract.

Data gathered at Cornell indicate that pups are born primarily in the tunnels; 30 of 42 pups (71%) whose births were observed were born in the tunnels, rather than in the nest box. At Michigan, 6 of 8 pups (75%) whose births were witnessed were born in the tunnels. During parturition, the breeding female is not obviously assisted by other colony members, although colony mates that encounter the female in the tunnels often stop to sniff at her before moving away. The newly born young are not immediately attended by either the breeding female or the breeding males. Instead, pups are cleaned and carried to the nest by nonbreeding colony members (see "Neonate Tending," below). Partu-
rition typically lasts 1–3 h (depending on litter size), with pups born every 10–30 min. Parturition and associated behaviors are also described in chapter 13.

NEONATE TENDING

Naked mole-rat pups are cared for by adult and juvenile colony members during the first 3–4 wk after birth. Care of pups consists of six behaviors:

1. Carrying pups
2. Grooming pups
3. Nudging pups
4. Pushing
5. Nursing
6. Sweeping pups

Carrying pups occurs when an adult grasps a pup with its incisors and either carries or drags (see “Transport,” p. 225) the pup through the tunnel system. Pups are typically grasped by the skin at the nape of the neck, although the belly or back may also be held (fig. 8-13).

When grooming pups, an adult grasps a pup with both forepaws and either licks the pup with its tongue or nibbles at the pup with its incisors. Grooming is most frequently directed toward the ano-genital area of the pup.

Nudging pups is a general contact with pups in which an adult either noses a pup with its muzzle or manipulates a pup with its forepaws.

When an adult shoves the blunt, anterior end of its muzzle (with the mouth closed) against the body of a pup, it is said to be pushing. The adult’s head vibrates rapidly side to side, and its body jerks forward with each push. As a result of contact with the adult’s muzzle, the pup is knocked several centimeters away from the adult, sometimes with such force that the pup is lifted into the air. Pushes are usually repeated in rapid succession such that the pup is often moved 15–20 cm. Pushing typically occurs in the nest box, although it is sometimes observed in the tunnels.

Fig. 8-13. An adult naked mole-rat carrying a pup. The pup is held between the adult’s incisors and lifted completely off the substrate while being carried through the tunnel system.
Fig. 8-14. A breeding female nursing her pups. Nursing begins when the female sits up or rolls onto her back, exposing her teats to the pups; nursing ends when the female pushes the pups away and rolls onto her stomach, thus preventing access to her teats.

Plate 8-7. A breeding female naked mole-rat nursing her pups in the center of a crowded nest box; these pups are about 3-days old. Photo: J.U.M. Jarvis.
Nursing of the pups is done only by the breeding female (fig. 8-14), although nonbreeding males and females sometimes develop enlarged teats just before parturition (Jarvis, chap. 13). Nursing begins when a female rolls onto her back or side, making her teats accessible. Pups apparently actively seek out and approach the female, and several pups nurse simultaneously. Nursing often occurs in the nest, with the breeding female and her pups surrounded by or even lain on by nonbreeding colony members (plate 8-7). Nursing ends when the female either rolls onto her stomach or pushes pups away with her forefeet.

Sweeping pups involves an adult kicking a pup with its hind feet, using a motion that appears to be identical to the sweeping behavior observed during the transport of nesting material or debris (see "Transport," p. 225). A pup may be kicked once or several times in rapid succession; repeated kicks usually result in the pup's being tumbled rapidly along a stretch of tunnel.

After birth, pups are cleaned and carried to the nest by nonbreeding colony members. The breeding female nurses the pups, and lactation continues for about 3-4 wk. During lactation, the breeding female and the colony's breeding males are the most frequent participants per capita in grooming, nudging, and pushing pups (Lacey and Sherman, chap. 10); nonbreeders, especially juveniles, sometimes perform these behaviors (see Jarvis, chap. 13).

An unusual aspect of pup care in H. glaber is the occurrence of pushing. This behavior occurs frequently when pups are present in the nest, and almost appears to be a form of aggression. However, because it is so regularly performed by breeding animals (i.e., the parents of pups), it seems unlikely that it is detrimental to the young (see Lacey and Sherman, chap. 10). Pushing is directed exclusively toward pups and young animals (< 1-yr old). Pushing may function (1) to move pups quickly to the periphery of the nest, thereby preventing them from being trampled by other colony members, (2) to move pups quickly out of the way of predators, (3) to enhance the peristaltic gut action of pups, or (4) to help enforce social dominance among colony members (see also Reeve and Sherman, chap. 11). None of these hypotheses has been quantitatively examined.

The rate of successful weaning of litters is discussed in chapter 13. Differences in the care given to successful (i.e., reared to weaning) and unsuccessful (i.e., not reared to weaning) litters are striking, such that the fate of a litter can usually be predicted within 24 h of birth. Pups in successful litters are regularly nursed by the breeding female and are kept in the nest box where adult colony members spend considerable time crouching and reclining with the young; these pups are quickly retrieved and returned to the nest if they fall or are knocked out of the nest box. In contrast, pups in unsuccessful litters are nursed infrequently and are often left in tunnels outside the nest box; in the tunnels, pups in these litters are often stepped on or swept back and forth by nonbreeders. We do not know why only some litters are successful, although one hypothesis is presented in chapter 13 (also see the Appendix). Once a pup dies,
cannibalism is frequently observed; adults also sometimes kill live pups (Jarvis, chap. 13).

**Juvenile-Specific Behaviors**

The ontogeny of pup behaviors and morphological development are described in chapter 13. Several behaviors were exhibited primarily by juvenile naked mole-rats or were exhibited by juveniles in unique contexts:

1. Wrestling
2. Dragging

Two or more wrestling pups roll and tumble together, often while batting or incisor fencing (plate 8-8). Wrestling can involve two to four animals.

In dragging, one pup grabs another (typically by the back of the neck, hindquarters, or tail) with its incisors and drags that individual through the tunnel system.

Juvenile-specific behaviors are first observed at about the time pups are weaned (ca. 3–4 wk after birth). These behaviors are common among littermates for the next 1–2 mo, after which their frequency gradually declines. Juvenile-specific behaviors cease entirely by the time the animals are about 2-yr old.

In addition to wrestling and dragging, juveniles also exhibit incisor fencing and batting; these behaviors resemble certain agonistic behaviors exhibited by adults (see p. 237) but do not occur in the same contexts (i.e., when contesting a piece of food, or during struggles associated with changes in reproductive

Plate 8-8. Juvenile naked mole-rats incisor fencing. These juveniles are about 2-mo old. Photo: D. Hammond, Cape Town Argus (South Africa).
status). Among the pups, incisor fencing and batting appear to occur in all contexts in which two or more pups interact.

**Interactive Behaviors**

Naked mole-rats spend considerable amounts of time in close proximity to one another; 74% ± 5% of data points per individual collected during scan sampling (n = 65 animals in three colonies at Cornell; ≥ 125 scans per animal, ≥ 10-min scan intervals) consisted of mole-rats in physical contact with one or more colony mates. As a result, interactions among colony members are common. Animals interact when they contact one another in the nest, as well as when they are resting in or moving through the tunnels. We observed six behaviors that occurred during interactions between individuals:

1. Nose pressing
2. Nuzzling
3. Ano-genital nuzzling and sniffing
4. Sniffing (at another animal)
5. Head deflecting
6. Pawing

In nose pressing, two individuals face each other with their heads slightly lowered and the blunt ends of their muzzles pressed together. The nose press is brief, typically lasting only 1–2 s.

During nuzzling, an animal rubs the sides of its muzzle against the body of a second individual. Often one side of the muzzle is rubbed several times in succession before switching to the other side.

In ano-genital nuzzling and sniffing, an animal of one sex sniffs and uses its muzzle to nudge the genitalia of an animal of the other sex. One animal may mount the head of another, so that the genitalia of the animal on top are in contact with the muzzle of the animal on the bottom. More commonly, both animals lie on their sides, head-to-tail, such that the genital area of each is in constant contact with the muzzle of the other (plate 8-9).

In head deflecting, an individual turns its head to the side and down, such that the area of the head near one ear is closest to the muzzle of the second animal.

An animal pawing another reaches out with one forepaw and repeatedly drags that appendage along the body of a second individual.

A variety of responses are observed when two mole-rats encounter each other in a tunnel. Individuals may simply bump into one another and then move apart, exhibiting no apparent interactive behaviors. Alternatively, contact may be followed by sniffing, nose pressing, and head deflecting, or individuals may interact agonistically (see below). It was our impression that nose
pressing was most frequently exhibited by the colony's breeding female, whereas head deflections were more frequent among nonbreeders (in particular, young animals) when they encountered the breeding female or a breeding male. Pawing occurred primarily when one mole-rat tried to pass another that was blocking a tunnel, nest, or food-box entrance. Ano-genital nuzzling typically occurred between breeding mole-rats, although nonbreeding animals occasionally participated (see Jarvis, chap. 13). Nuzzling was observed during all phases of the female's reproductive cycle, particularly when the breeding female was in estrus.

**Agonistic Behaviors**

Naked mole-rats exhibit agonistic behaviors in several contexts, including competition for food or other resources (e.g., access to a digging site), defense of the colony against foreign mole-rats, competition for breeding status, and stimulation of colony-maintenance activities by the breeding female. There are seven types of agonistic interactions:

1. Open-mouth gaping
2. Incisor fencing
3. Batting
4. Biting
5. Shoving
6. Tugging
7. Tetany
Two animals engaged in open-mouth gaping stand face to face, with their muzzles almost touching. Both individuals open their mouths, with the top and bottom incisors separated (fig. 8-15; plate 8-10). Air is then rapidly inhaled and exhaled through the open mouth, producing a hissing sound (Pepper et al., chap. 9).

Incisor fencing occurs when two mole-rats stand face to face, with their mouths at right angles and their incisors locked together. The incisors may be released briefly, allowing the animals to reposition their heads before locking incisors again (fig. 8-16). The animals typically shove back and forth against each other and rock their heads from side to side while the incisors are locked together. Incisor fencing in juveniles is depicted in plate 8-8.

Two animals that simultaneously swat at each other’s muzzles with their forepaws are batting. The forefeet may also be placed on the other individual’s muzzle and held there, preventing the second animal from contacting the muzzle of the first.

In biuung, the jaws of one animal close on the body of another individual (see plate 8-10).

Shoving occurs when two mole-rats stand face to face, with their heads slightly lowered and the blunt ends of their muzzles pressed together. One
Plate 8-10. Top, Mole-rats threatening each other with open-mouth gapes (accompanied by hissing). The animals on the left and right are from different colonies. Bottom, Open-mouth gapes can occur at close range and may precede biting. Again the individuals are from different colonies. Photos: R. A. Mendez.
animal moves forward, pushing the second animal backward for a distance of up to 1 m. The animal doing the shoving frequently hisses (Pepper et al., chap. 9) while performing this behavior. Participation in shoving is analyzed in chapter 11.

A tugging individual grasps the skin of another with its incisors and pulls backward, often while bracing against the sides of the tunnel with its feet (plate 8-11). The nape of the neck, the loose skin on the hips, and the tail are most frequently grabbed by another individual.

Tetany occurs when an individual doubles up and lies perfectly still, often with its feet in the air (plate 8-12). Tetany is a response to being shoved or gaped at by the breeding female. Individuals may remain in this contorted posture for several minutes, long after the interaction with the breeding female has ended.

Within colonies, agonistic behaviors associated with competition for resources (incisor fencing, tugging) and reproductive dominance/colony-activity stimulation (shoving) do not result in injury to either participant. In contrast, agonistic interactions associated with colony defense (biting) and competition for a breeding vacancy among females (batting, tugging, and biting) do sometimes result in injury and death. During 1981–1986, a total of 12 animals in four colonies (at Cornell) died as a result of injuries received during fights following the removal of a breeding female (Lacey and Sherman, chap. 10); deaths resulting from struggles for breeding opportunities have also been reported by Jarvis (chap. 13) and Faulkes et al. (chap. 14). Agonistic interactions
Plate 8-12. A small nonbreeding naked mole-rat (left) exhibiting the tetany posture after having been shoved and gaped at by the breeding female (right). Photo: R. A. Mendez.

associated with resources are usually accompanied by a loud chirping vocalization (see Pepper et al., chap. 9), whereas agonistic interactions associated with colony defense or reproductive status are accompanied by a hissing sound.

All 12 animals at Cornell that died as a result of agonistic interactions were ostracized before their deaths. Once injured, these animals were excluded from the colony’s nest box and were attacked by other colony members, particularly the breeding female, if they attempted to enter the nest. These shunned animals subsequently crouched and shivered in the corner of an empty box or toilet; these mole-rats rarely attempted to leave the empty box and frequently failed to show any response when approached by other colony members. Death of the injured animal typically followed within 2–3 days of its being excluded from the colony’s nest box. Even when removed from their colony and provided with a localized heat source and ad libitum food (see Jarvis, Appendix), these individuals usually died in a few days; it was never possible to reintroduce them to their colony without reinitiating aggressive behaviors by the breeding female and other colony members.

**Alarm Reactions**

Naked mole-rats respond strongly to disturbances such as loud noises, vibrations, and the introduction of foreign objects. Responses to such disturbances, termed alarm reactions, include:
1. Freezing
2. Scrambling

In freezing, an animal suddenly ceases all activity, holding itself in the same position it had been in at the time of the disturbance.

Scrambling occurs when numerous colony members simultaneously dart (see "Locomotion," p. 223) forward and backward in the tunnels or nest box, with no single coordinated direction of locomotion evident among individuals.

The alarm reactions of naked mole-rats fall into two categories: those elicited by sudden environmental disturbances (e.g., bumping the tunnel system, slamming the door), and those elicited by more minor disruptions (e.g., the introduction of food). Major disturbances elicit an immediate response by all colony members: the mole-rats freeze, and then begin scrambling, typically while trying to exit the nest and immediately adjacent tunnels. Unweaned or recently weaned pups may be carried from the nest during scrambling, or they may be trampled. In the absence of further stimuli, scrambling gradually ceases and is replaced by less frenzied forms of locomotion (e.g., walking and running). Colony members slowly return to the nest and resume activities unrelated to alarm reactions.

In contrast, reactions to introduced objects (e.g., food, snakes, or unfamiliar conspecifics) are less immediate; rather than the explosion of activity associated with scrambling, reactions to introduced objects consist of a gradual increase in colony activity. Animals encountering the stimulus typically approach it several times using the crouch advance (see "Locomotion," p. 223) and sniff briefly at the object before retreating. If the object is food, some colony members begin feeding, followed by tugging and incisor fencing as colony mates arrive in the vicinity. If the object is a snake, the animals may hiss (Pepper et al., chap. 9) or bite at it, and some recruitment of (larger) nonbreeders may occur. If the object is an unfamiliar conspecific, one of the first individuals to contact it will give a trilled vocalization (Pepper et al., chap. 9) while running back toward the nest; this results in an increase in colony activity and recruitment to the site of the developing conflict (see Lacey and Sherman, chap. 10).

Summary

A total of 72 nonvocal behaviors exhibited by naked mole-rats have been characterized. These behaviors have been grouped into 17 categories according to presumed functional similarities. As such, these categories represent hypotheses regarding the adaptive significance of individual behaviors. The behavioral repertoire of *Heterocephalus glaber* is clearly complex, and we suspect that many subtleties of the animals' behavior remain to be discovered. Elucidating
the adaptive significance of individual behaviors is essential to understanding the complex, cooperative social organization of *H. glaber*.

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