CHAPTER 5

BURROWS AND BURROWING BEHAVIOR BY MAMMALS

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1. INTRODUCTION

Most mammals use shelter of some sort either daily or seasonally. For some species the shelters are simple, consisting of the shade of a tree or the lee of a rock. Many other species, however, construct or expropriate elaborate dens, nests, or burrows which provide many benefits to the resident. Costs are also incurred when constructing or obtaining burrows, and these must be offset to make the acquisition advantageous. In this chapter we will concentrate on the characteristics, advantages, and disadvantages of burrows and discuss some of the anatomical, physiological, and behavioral traits associated with all degrees of fossorial behavior, from species which use very simple burrows to those taxa which are primarily subterranean (we will use the term fossorial for burrowing mammals and subterranean for those taxa that spend almost all of their lives below ground).

A considerable amount of information on these topics is embedded in the natural history literature on mammals and therefore a taxonomic survey of burrowing behavior will not be included (readers are referred to such sources as the American Society of Mammalogists Mammalian Species series, Walker [1983], Smithers [1983], etc., for details of the burrow-
ing habits of specific genera or species). Rather, we will concentrate on broad features associated with burrowing and use specific taxa as examples. Nevertheless, certain mammals possess traits which necessitate their being discussed as a group (e.g., the completely subterranean taxa, which are primarily confined to a few families).

A significant number of mammalian species construct nests or dens that do not involve excavations into the soil and these species will not be included in this review. For example, many squirrels and other rodents use hollow trees or leaf nests above ground. Even some large primates construct temporary resting sites among the trees (e.g., Goodall, 1986). Other mammals use existing structures such as fallen logs or rock crevices, or build elaborate stick dens on the ground (e.g., woodrats, Australian stick-nest rats) or in water (muskrats, beavers). While some of these structures may include slight incursions below ground, the majority of the structure is above ground.

Burrowing probably has been used by mammals since early in their origins. Fossil evidence points to morphological adaptations for a fossorial existence (Webb, 1966; Rose and Emry, 1983) and actual fossil burrows have been identified (e.g., Vorhies, 1974). Three orders of mammals (Marsupialia, Insectivora, and Rodentia) have some members that are entirely subterranean. Furthermore, the members of many subfamilies of murids (the taxonomy of Anderson and Jones, 1984, will be used in this chapter) are primarily subterranean as are all of the members of the families Geomyidae, Ctenomyidae, and Bathyergidae (Ellerman, 1956; Nevo, 1979). These groups, as well as others that spend smaller fractions of their lives below ground, will be discussed in this chapter.

The soil obviously is the major raw material for shelter construction in most terrestrial habitats. It provides effective physical protection and for many mammals it also supports the plants and animals, primarily insects, that many fossorial mammals use. Many species of burrowing mammals are limited in their distribution by their relationship with specific soil types. While the below-ground environment is benign or even beneficial to many species, it also offers physical and physiological challenges that must be met for the successful occupant.

We will begin with generalizations about the advantages and functions of burrows for mammals. Subsequently, we will discuss some of the costs associated with burrow construction and the adaptations of mammals for burrowing. Finally, we will consider interactions within and between burrow residents and the effects of burrows on the environment. The information presented in this chapter will be biased toward our own research experiences and knowledge of North American mammals, especially rodents, but attempts have been made to secure information for other continents and taxa.
2. CHARACTERISTICS AND ADVANTAGES OF MAMMALIAN BURROWS

Shelter is the basic function of a burrow for most mammals and structures limited to this use tend to be relatively simple. As other functions are incorporated into the role of burrows, such as food gathering and storage, burrows tend to become more complex such that mammals whose entire existence is maintained underground produce very elaborate structures.

2.1. Shelter: Protection from the Environment and Predators

The vast majority of fossorial mammals use burrows simply as a place to stay when not foraging, searching for mates, or defending their territories. Even so, these taxa spend a substantial portion of the day underground (usually well over half the day and frequently much longer than that; e.g., Kenagy, 1973). The advantages of using burrows, even if just for shelter, are clear because the burrow environment is significantly more moderate than the above-ground environment. For example, soil temperature fluctuates much less even a few centimeters into the soil than it does at the soil surface (Kenagy, 1973; Kay and Whitford, 1978). At a depth of approximately 30 cm, almost all daily temperature fluctuations disappear (although long-term seasonal changes in temperature do occur; Reichman et al., 1985), so that the insulating qualities of the soil are advantageous during both extremely hot summers and cold winters. Burrows also protect their inhabitants from wind, rain, and snow during inclement weather. Many mammals seal off the burrow entrances while in the burrow, further isolating them from the above-ground environment (e.g., Vorhies and Taylor, 1922).

Most burrows contain nests—expanded chambers which may be lined with vegetation (Vorhies and Taylor, 1922; Hickman, 1983a, b) or fur (Hall and Meyers, 1978; Kolb, 1985) to keep the residents dry and warm. The beneficial features of nests for individuals are compounded when females give birth and the young, which may be relatively helpless and possess poor thermoregulatory abilities, stay in the nest for days or weeks.

Burrows also offer effective protection from many predators. Avian predators are excluded from burrows and most terrestrial carnivores cannot chase their prey down small burrows. Weasels and férrets do go into burrows after rodents (Smith, 1967; Cloark, 1977; Hoogland, 1981; Halpin, 1983) and some carnivores, such as badgers, dig their prey out of burrows (Smith, 1967; Knopf and Balph, 1969; also see Section 3.2 on the disadvantages of burrows). Plugging the burrow may inhibit some snakes from entering but other species will dig through the plugs (Hickman,
1973) and may actually be drawn to fresh soil as an indication of recent excavations by potential prey (Brett, 1990; Jarvis, 1990).

Burrows that provide basic protection can be quite simple, consisting of little more than an entrance, a short tunnel, and perhaps an expanded nest. The vast majority of mammals that construct burrows use such simple designs, so there are hundreds of references to these types of burrows in the literature. Here we will describe just a few examples of basic protective burrow systems.

An example of the simplest type of excavation that serves for protection is exhibited by the Namib golden mole (Eremitalpa granti namibensis) and the marsupial mole (Notoryctes typhlops). These two species tunnel through dunes whose loose, sandy soil will not support a permanent burrow. Thus, as the animals push through the sand ("sand swimming"), their excavations collapse behind them. The golden mole apparently comes above ground for just a few hours each night to look for prey (Holm, 1969). The marsupial mole has a similar habit, but the females may excavate deeper, more permanent galleries when they give birth (Walker, 1983). Both species may seek food (insects, lizards) underground, but it appears that they forage primarily on the surface, relegating the digging to a protective function.

Many large mammals construct simple, linear burrows. For example, platypuses construct tunnels into the banks of rivers or ponds (Grant, 1983). Insulated nests at the ends of burrows are especially important in protecting both adults and offspring from thermal extremes. Armadillos excavate burrows that are up to 1.25 m long, straight, and angled slightly into the ground, and terminate in a simple nest (Taber, 1945; Clark, 1951). Pangolins build similar burrows that may extend more than 3 m (Walker, 1983). Very few rabbits construct burrows but the pygmy rabbit (Brachylagus idahoensis) does dig simple tunnels with five to 10 entrances (Green and Flinders, 1980). Carnivores such as honey badgers, weasels, polecats, and genets use similar tunnels, although suricates and mongooses, living communally, may excavate longer and somewhat more elaborate structures (Smithers, 1983). Aardvarks dig several types of burrows, one of which is for foraging. Two others, however, provide mainly shelter. One is a temporary refuge only 1–2 m long but the other is used for longer periods, may be up to 13 m long, and may have several openings (Smithers, 1983).

Among mammals, rodents excavate the most elaborate burrow systems that are used primarily for protection (Fig. 1). These burrows frequently have several openings, interconnect below ground, and have more than one nest. For example, Butynski and Mattingly (1979) found the average depth of springhare burrows to be 78 cm and the average length to be 42 m. Springhares live in groups and apparently are constantly expanding their burrows (Fig. 1A). Gunnison prairie dog burrows

372
BURROWING MAMMALS

FIGURE 1. (A) The burrow of a springbok. (Redrawn from Butynski and Mattingly, 1979.) (B) Several prairie dog burrows. (Redrawn from Longhurst, 1944.)

(Fig. 1B) tend to have two or more entrances and consist of tunnels a few meters long (Longhurst, 1944). The burrows usually have several major branches and a number of small, side branches at the end of which nests are located. Sheets et al. (1971) excavated 18 prairie dog burrows that ranged from 1 to 3.6 m deep and 3.5 to 28 m long. The burrows made an abrupt vertical descent from a crater-shaped opening before leveling off. Ognev (1947) followed the maturing of suslik ("Citellus") burrows in Russia (Fig. 2). The burrows began in the first summer as simple excavations which ramified in subsequent years as new segments were constructed and old ones were filled in. Reynolds (1988) describes the burrow systems of four unrelated species of rodents in Idaho and found that although all were quite simple, each had distinct design features.

Even though the burrows used for protection from the environment and predators tend to be relatively simple, they clearly play a large role in the lives of the mammals inhabiting them. Even mammals using the sim-
plest burrows spend the majority of their lives in them and thus are relatively warm in the winter, cool in the summer, humidified in the dry seasons, and safe from predators. Thus, if a mammal has no particular reason to be above ground (such as foraging, maintaining a territory, or searching for a mate), it might be expected to stay in its protective burrow.

2.2. Food Storage

Some mammals extend the protective function of their burrows from self-protection to the protection of food they have gathered (Smith and Reichman, 1984). Many simple burrow configurations are also effective in protecting food so that with only modest expansion, a simple burrow will suffice for the additional role as a site for food storage.

Food kept in a burrow can be protected from a number of sources of loss. For example, by gathering and storing large quantities of food an individual can secure the resource before it can be expropriated by a competitor. Furthermore, caching allows a mammal to take advantage of abundant food resources during one season while avoiding the environmental extremes of another. Food storage may also preclude a cache from having to forage when predators are especially active or abundant.

Very few mammals other than rodents use their burrows just for shelter and food storage (Smith and Reichman, 1984). Some shrews cache captured prey in shallow tunnels or runways under rocks or logs. In some cases, they immobilize their prey and cache them alive until they can return to them (Martin, 1984). Bears, mustelids, leopards, and hyenas occasionally bury their prey (Smith and Reichman, 1984), but these mammals do not live in burrows (although bears may use dens in the winter).
FIGURE 3. Top and a lateral view of several relatively simple kangaroo rat (Dipodomys microps) burrows. (Redrawn from Anderson and Allred, 1964.)

Many of the references to food-storing behavior by rodents in the publications of Ognev (1947) and Smithers (1983) allude to simple lateral extensions of burrows which function as cache sites. Such caches resemble nest locations but contain food rather than nest material. Some of the smaller species of kangaroo rats exhibit this pattern of burrow use (Fig. 3; Tappe, 1941; Anderson and Allred, 1964) and dozens of references in the natural history literature on rodents suggest that this is a common pattern in rodents. Clearly, with the addition of slightly more room in a burrow, it becomes an effective storage site, especially when the alternative is loss of food or the obligation to forage in a hostile environment.

Some rodents do more than just expand simple burrows for food storage. For example, grasshopper mice (Onychomys) maintain nest burrows in which they sleep and rear their young but they also construct separate caching burrows in which they place piles of seeds until they are used (Ruffer, 1965). However, the grasshopper mice, which are carnivorous, were never seen to cache insects or other mice. Other species that maintain home burrows and hoard food elsewhere include chipmunks (Thomas, 1974; Shaffer, 1980) and acouchis (Morris, 1962). Some of the smaller species of kangaroo rats (Dipodomys) make hundreds of shallow depressions around their burrows in which they place seeds for later use (Fig. 4; Shaw, 1934).

A few species of rodents construct elaborate burrow systems in which they reside and store their food. One of the best known is the bannertailed kangaroo rat (Dipodomys spectabilis). Monson (1943) and Vorhies and Taylor (1922) present extensive data on the structure of the burrows and the nature of the caches made by these kangaroo rats. The rodents construct elaborate mounds that are raised from 20 to 78 cm and extend at least that far into the ground, taking the form of a saucer inverted atop
another (Reichman et al., 1985). The rodents produce the mounds by periodically kicking dirt from around the apron of the structure up onto the mound, a process that may take 2 years to complete (Best, 1972). The mounds are honeycombed with tunnels and cavities (Fig. 5) which occasionally collapse, requiring extensive repair by the rodents. Hundreds of thousands of seeds may be stored, in species-specific piles, within the
labyrinthine mound (Vorhies and Taylor; 1922). The caches tend to be concentrated in a band 30 cm below the mound surface and at depths greater than 50 cm (Reichman et al., 1985). Other species of the large kangaroo rats exhibit similar burrow construction and food storage characteristics (Shaw, 1934; Hawbecker, 1940).

2.3. Foraging

While no mammals spend their entire lives underground, one species of marsupial, two families of insectivores, and several families of rodents contain members that carry out almost all of their activities underground. Furthermore, all the members of three rodent families are essentially subterranean (Ellerman, 1956; Nevo, 1979). Thus, they add foraging to food storage and self-protection as a function of the burrow system (it should be noted that very little is known about where subterranean forms mate). These taxa exhibit the most elaborate anatomical, physiological, and behavioral traits associated with a subterranean existence (Nevo, 1979). Other rodent species no doubt occasionally harvest below-ground resources such as seeds, bulbs, tubers, or corms, but do not regularly forage below ground.

One of the least known of the subterranean forms is the marsupial mole (Notoryctes). It forages for insects, their larvae, and worms, and thus has converged ecologically on the insectivores (Walker, 1983). Its burrow collapses behind it as it digs, precluding the maintenance of a discrete burrow system.

Two families of insectivores are primarily fossorial. The Chryschlorididae includes the Namib golden mole (Eremitalpa granti namibensis), which is similar to the marsupial mole in that it digs in sand dunes that collapse behind it. The golden mole apparently does forage in the sand for termites, but also comes to the surface to hunt for insects and lizards (Holm, 1969). It sleeps below ground but apparently not in a discrete chamber (nothing is known about where females raise their young). Other genera of this family live in soils that support permanent burrows and therefore leave extensive tunnels in the wake of their foraging trips. Chryschloris stuhlmanni excavates long burrows between clumps of vegetation and then concentrates its burrows around the bases of shrubs or clumps of bamboo, apparently where insect larvae congregate (Fig. 6A; Duncan and Wrangham, 1971; Jarvis, 1974). Its burrows run less than 4 cm below the surface, leaving behind typical raised ridges of soil; apparently no deep tunnels are excavated so no mounds of cast soil occur around the burrows. Amblysomus hottentotus makes burrows that are similar in configuration but which include segments deeper than those of Chryschloris (Fig. 6B; Kuyper, 1985).

The true moles (Talpidae) are the most diverse group of insectivores
that spend their lives below ground. Talpids rarely come above ground; rather they use their burrows for protection and the acquisition of food, and a few species even store earthworms (Funmilayo, 1979). Moles dig burrows characterized by a long segment that has many side branches and occasionally one or more complete loops (Fig. 6C–D; Hickman, 1983a,b, 1984a). A burrow of Scalopus aquaticus was 185 m long, including one 36-m segment that was blocked from the remaining portion (Hickman, 1984a). Few surface ridges were evident, and one bolt hole was noted 39 m from the nest. The nest was approximately 20 cm deep and was lined with dead, compacted leaves. A burrow of Parascalops breweri was similar in configuration (Fig. 6D) but was much longer (550 m; Hickman,
A nest with two entrances was found 10 cm below the surface and was packed with dry leaves and grass (Hickman, 1983a). Other authors noted a similar burrow structure, but with deeper nests (Eadie, 1939; Wright, 1945). Wright (1945) also observed one system that was in use for over eight years, presumably by the same individual. Burrows of Condylosciscristata, a semiaquatic mole, were similar to those of the other moles, although the burrow tended to parallel moist areas (Fig. 6E; Hickman, 1983b). One burrow was 72 m long while another along a lake front totaled 270 m. Both burrows contained a single nest lined with dead, dry material (Hickman, 1983b). Data and drawings presented by Ognev (1947) reveal that the Eurasian moles exhibit similar burrow patterns.

While moles are generally restricted to their burrows, they apparently come above ground occasionally as is evidenced by their presence in owl pellets (Giger, 1965; Choate, 1971; Hallet, 1978). Moles may travel above ground to disperse (J. Patton, pers. commun.), but we could not find any indication of this in the literature. They may also come above ground to mate, but Glendenning (1959) suggests that males build lateral tunnels to intercept the burrows of females. This total reliance on a subterranean existence is not surprising as morphology of moles suggests that they would be ungainly on the surface.

Among rodents, two families contain members that are primarily fossorial, and four others are entirely subterranean (Nevo, 1979). Only one genus in the family Octodontidae (Spalacopus) possesses many of the traits of other primarily fossorial rodents (Reig, 1970; Walker, 1983). The rodents make extensive tunnels which are from 5 to 7 mm in diameter and from 10 to 12 cm deep and they live in small colonies.

The large family Muridae contains several genera that have members that are primarily fossorial, but little is known about their burrows and burrowing habits. Walker (1983) briefly describes the characteristic burrows and surface mounds associated with burrow excavation in the genera Myospalax, Prometeomys, and Ellobius, and he suggests that the latter is the most specialized fossorial microtine rodent. Apparently all of these genera feed on below-ground plant parts, although Walker (1983) indicates that they may occasionally come above ground to forage. The water vole (Arvicola terrestris) excavates burrows that are up to 200 m long and 30–60 cm deep (Fig. 7; Airoldi, 1976). The burrows tend to be linear and dispersed when population densities are low, but more convoluted and clustered when densities increase. One or two nests are associated with each burrow system (Airoldi, 1976). J. P. Airoldi (pers. commun.) also noted that in certain populations, burrow systems tend to coalesce forming very long and complicated systems that may include 200 residents.

Three families of rodents (Geomyidae, Ctenomyidae, and Bathyergidae) and two subfamilies of murids (Spalacinae, Rhizomyinae) appear to be composed completely of subterranean forms (Nevo, 1979). These
representatives have converged remarkably in structure and exhibit strikingly similar burrow patterns (Fig. 8; Genelly, 1965; Jarvis and Sale, 1971; Hickman, 1977b, 1983c; Reichman et al., 1982; Beyene, 1986; Davies and Jarvis, 1986; Brett, 1990). Because they are so similar, we will briefly discuss their shared traits. All are herbivorous and feed primarily on below-ground plant parts, although some will feed above ground for short periods or pull above-ground vegetation underground. Members of the Bathyergidae appear to specialize on the below-ground parts of the diverse geophyte flora of South Africa, frequently gathering and eating thousands of bulbs, tubers, or corms (Lovegrove and Jarvis, 1986). Naked mole rats (Bathyergidae, Heterocephalus glaber), which live in large colonies, locate and consume huge tubers weighing dozens of kilograms (Brett, 1990). Probably because of their feeding habits, all of the rodents tend to construct feeding burrows that lie in the root zone (usually 10–60 cm deep), although Bathyergus suillus, the largest subterranean rodent (up to 1.8 kg), makes extensive burrows beneath the root zone (Davies and Jarvis, 1986; Lovegrove and Jarvis, 1986). Many of the highly fossorial species cache large quantities of plant material in their burrows.

Most of the burrows contain one or more bolt holes, deep extensions that apparently serve as escape tunnels. The burrow systems all contain one to several nests, and in one pocket gopher system (Thomomys bottae) males and females were found to share common nests that contained pups while maintaining separate burrow systems (Reichman et al. 1982).

Davies and Jarvis (1986) present an important summary of the characteristics of burrows of these rodents that carry out almost all of their ecological functions below ground, and the authors kindly consented to allow their table to be included herein, with minor modifications (Table I). Clearly these rodents, along with the moles and golden moles, represent the most specialized fossorial forms among the mammals. Because these taxa, which have evolved on several continents, live in similar, relatively stable environments it is tempting to suspect that many of their shared traits are unique to the subterranean forms and are highly convergent (Nevo, 1979). This may be true for some anatomical traits associ-
FIGURE 8. Drawings (redrawn from originals) of representative rodent burrows. Figures A, E, and G are burrows of Tachyoryctes. (From Beyene, 1986; Hickman, 1983c; Jarvis and Sale, 1971, respectively.) Figure B is Heterocephalus. (From Brett, 1988.) Figure C is Pappogeomys castanops. (From Hickman, 1977a.) Figure D is Cryptomys hottentotus. (From Hickman, 1979.) Figure F is of Bathyrurus suillus. (From Davies and Jarvis, 1986.)

ated with frequent digging, but other traits (e.g., behavioral, physiological, genetic) are shared with other mammals and may not be the direct result of selection pressures associated only with the underground habit (see, e.g., Patton and Yang, 1977 and Patton et al., 1979 for a discussion of this consideration in relation to genetic variation and speciation).

2.4. Underground Environment

The preceding sections characterized traits of the burrows of several groups of mammals. The burrows and the particular features of the mam-
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<th>Av. mass/burrow system (g)</th>
<th>Av. burrow length (m)</th>
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<td>2120</td>
<td>1</td>
<td>300 - 1000</td>
<td>20</td>
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<td>63 - 33,600</td>
<td>Yalden, 1975</td>
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<tr>
<td>Batyergidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Jarvis and Davies, unpubl.</td>
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<td>933</td>
<td>1</td>
<td>877</td>
<td>256</td>
<td>4</td>
<td>1390 - 3496</td>
<td>0.2 - 1.2</td>
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<td>2 - 14</td>
<td>132 - 810</td>
<td>464</td>
<td>4</td>
<td>3922</td>
<td>13.2 - 189</td>
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<td>2 - 3</td>
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<td>181</td>
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<td>2550</td>
<td>150 - 1052</td>
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<td>Heliophobius argenteocinereus</td>
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<td>Hickman, 1979</td>
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<td>21</td>
<td>60</td>
<td>1250</td>
<td>595</td>
<td>2</td>
<td>5401</td>
<td>7.4 - 588</td>
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<td>Ctenodactylidae</td>
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<td>Jarvis and Beviss-Challinor, unpubl.</td>
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<td>Ctenomys talcarum</td>
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<td>156</td>
<td></td>
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<td>207 - 32,400</td>
<td>17.143 - 47.034</td>
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<td>C. optimus</td>
<td>439</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>5</td>
<td>272 541</td>
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<tr>
<td>C. peruvanus</td>
<td>562</td>
<td>1 to several</td>
<td>1082</td>
<td>800</td>
<td>45</td>
<td>2267</td>
<td>10.704</td>
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</table>

*In some cases, the approximate burrow lengths and home ranges were calculated from the literature, the latter by determining the area contained within irregular polygons completely enclosing maps of burrow systems. The biomass per hectare has, in most cases, been calculated from density figures in the literature.

Source: Data are from Davies and Jarvis (1985).
mals that inhabit them are, however, influenced by the physical conditions of the soil and the ambient atmosphere within the burrows.

As noted earlier, the soil is an excellent insulator, buffering soil residents from the extreme variation exhibited in the above-ground environment. For example, Kennerly (1964) recorded ambient temperatures in summer in Texas of 23–58°C while burrow temperatures were only 28–32°C. At the opposite extreme, Mayer (1955) found temperatures in the burrows of hibernation ground squirrels (Spermophilus tridecemlineatus) in Alaska to range between −1°C and −9°C while outside temperatures went from 5°C to −41°C.

The moisture content of the soil is important to burrowing mammals for several reasons. For some species, excavation is either more cost-effective when the soil is moist or only possible under moist soil conditions, especially where the soil becomes extremely hard when dry (Jarvis and Sale, 1971; Elliott, 1983; Brett, 1990). Soil moisture, even when very low, is also responsible for maintaining high burrow vapor pressures (Kay and Whitford, 1978). When the soil becomes saturated, however, flooding can occur and burrowing mammals can be trapped in their tunnels and drowned. One of us (OJR) observed such circumstances for pocket gophers, prairie dogs, and golden moles and numerous authors have noted this phenomenon (e.g., Hickman, 1983a,c). Reichman and Baker (1972) described a system in which the pocket gopher Thomomys bottae was alternately restricted to moist soils near a stream and drowned or displaced by another species when the stream flooded every year or two.

The physical features of soil also affect whether mammals can construct burrows and, if so, what their characteristics are. As already noted, the marsupial mole and the Namib golden mole burrow in sand that collapses in their wake, severely restricting the type of excavations they can make. Soils that are too hard may entirely restrict burrowing by mammals or limit the diversity of mammals inhabiting the area. For example, the naked mole rat is the only subterranean mammal living in the extremely hard red soils of east Africa (Brett, 1990; Jarvis, 1990). These rodents live in moderate- to large-sized colonies and take turns digging. It has been suggested that the distribution of their resources and the need for cooperative digging in the hard soils is related to the eusocial life-style exhibited by these rodents (Sherman et al., 1990). While it is not known with certainty that other species cannot dig in the hard soil, it is known that they do not occur where the soil is hardest. Of course, the presence of many rocks or large rocks may also inhibit burrowing (Hansen and Morris, 1968).

Many studies of rodents have revealed microhabitat preferences based on soil types. Four species of pocket gophers studied by Miller (1964) occurred in a nested pattern of soil use with specialists sequentially excluding more generalist species along a soil gradient, and Best
(1973) found a similar pattern with three pocket gopher species in New Mexico. Thaelor (1968) also found pocket gophers segregated by soil type but notes that the species were not always in the same soil types in different areas, suggesting that the segregation is not absolute.

The burrow environment itself can be characterized as dark, moist, of moderate temperature, and possessing a skewed ratio of oxygen and carbon dioxide. Even burrows that are left unplugged become dark shortly past the entrance. Burrow walls absorb light effectively and preclude it from reaching deep into a burrow system. Of course, burrows that curve sharply or are plugged restrict light even more. The absence of light restricts vision, which may account for the loss of eyesight by several taxa over time.

Even open burrows maintain a relatively high moisture content, although Schmidt-Nielsen and Schmidt-Nielsen (1950) noted that relative humidity dropped to 30% in open kangaroo rat burrows. Plugged burrows quickly reach 100% RH, even when soil moisture is extremely low (Kennerly, 1964). The high moisture content is probably advantageous, especially in arid environments where evaporative water loss may be significant above ground (although high relative humidities may restrict evaporative cooling in animals, which may be a problem for individuals with excessively high body temperatures). Not only would high moisture content in a burrow (Kay and Whitford, 1978) reduce water loss by the resident, but seeds stored in the high humidity would absorb moisture (Morton and MacMillen, 1982), thereby actually providing preformed water to consumers (Frank, 1988).

Vogel and Bretz (1972) and Vogel et al. (1973) detailed the characteristics for an effective passive ventilation system for open burrows and showed that prairie dogs incorporate such designs into the construction of their burrows. Of course, air flow in plugged burrow systems is significantly more restricted. When mammals are in their sealed burrows their activity is probably reduced (e.g., while they are sleeping), minimizing the need for extensive gas exchange with the above-ground atmosphere.

Animals that are entirely subterranean usually keep their burrows plugged and thus must rely on diffusion of oxygen and carbon dioxide across the burrow wall to maintain appropriate levels of these gases in the burrows. Kennerly (pers. commun.) suggested that the minimum length of a pocket gopher burrow may be determined by the surface area required to maintain adequate levels of oxygen for the burrow resident. In this light, it would be very interesting to analyze the respiratory characteristics of the marsupial mole and Namib golden mole, which live in sand and have only the tiny air space around their bodies to rely on.

Gas diffusion models have been used to identify and quantify the various factors that impinge on respiratory gas concentrations in mammal burrows (Wilson and Kilgore, 1978; Withers, 1978). Arieli (1979) outlined
some of these factors, which include the oxygen consumption and carbon
dioxide production rate of burrow residents, airing behavior (pumping) of
the resident, soil water content, depth and design of the burrow system,
ambient temperature, absolute pressure differences between the burrow
air and the outside air, and physical characteristics of the soil. Arieli
(1979) also presented a table with burrow gas data for 14 species of fos-
sorial mammals and discussed how the figures relate to the factors listed
above.

The gases in burrows of mammals that are not strictly subterranean
also differ from those in ambient air conditions. For example, Studier and
Proctor (1971) found reduced oxygen levels and increased carbon dioxide
concentrations in the burrows of the 13-lined ground squirrel, and Soholt
(1974) noted that increased activity by kangaroo rats (Dipodomys mer-
riani) significantly increased the carbon dioxide : oxygen ratio in simula-
ted burrows. The most extreme differences between burrow and ambient
air gas concentrations occur in hibernating squirrels (Spermophilus par-
ryi) and marmots (Marmota breweri) (Williams and Rausch, 1973). The
authors report CO₂ levels of 13.5% and O₂ concentrations of 4%. Such
extreme values suggest that many burrowing mammals must have effec-
tive adaptations for such conditions, and these will be discussed in a later
section. In the sealed burrows of subterranean species CO₂ levels also
reach high concentrations. For example, Arieli (1979) reported CO₂ con-
centrations of 4.8% in the burrows of Spalax ehrenbergi.

Interestingly, respiratory gas concentrations in the shallow burrows
of moles appear to vary little from those in ambient atmospheric con-
centrations. Olszewski and Skoczen (1965) note that the wind speed over
fresh ridges and mounds thrown up by moles directly affects oxygen
concentrations in the mole burrows, and Schaefer and Sadleir (1979) actu-
ally found O₂ levels higher and CO₂ levels lower in mole burrows than in
the surrounding air.

3. COSTS AND DISADVANTAGES OF BURROWING

While the widespread use of burrows by many mammals and the
specializations of those that are entirely subterranean suggest that bur-
rowing is advantageous, burrowing is not without its costs and liabilities.
Some of the disadvantages of burrowing involve simple energetic costs
which must be factored into cost–benefit considerations of the adaptive
advantages of burrowing. Other costs involve evolutionary trade-offs that
can be ameliorated by anatomical and physiological adaptations and by
behavioral adjustments.
3.1. Energetic Costs

The cost of excavating and maintaining a simple, shallow burrow system is probably not high compared to other metabolic costs for a mammal; especially if averaged over the lifetime of the burrow. In fact, some mammals (e.g., armadillos; Taber, 1945; Clark, 1951) dig simple burrows almost every night, suggesting that the costs are so low (or benefits so high) that the mammal can afford to excavate fresh burrows as needed. The more extensive or complicated the system is, however, the longer it will take to excavate and the more the burrow system will cost. For example, Vleck (1979, 1981) calculated that it costs a pocket gopher $360-3400$ times as much to dig $1$ m (depending on the soil type) as it does to walk the same distance. Andersen (1982) analyzed the costs of digging a burrow in relation to its geometry and dimensions, and found that minimizing the diameter of a burrow is especially important in reducing overall excavation costs. The cost of a burrow increases beyond the mere excavation costs when further investments, such as nests and cached food, are added. It should be noted that many elaborate burrow systems are inherited (e.g., Jones, 1984) and thus the costs are not necessarily incurred each generation.

The value of an incomplete burrow system to a mammal that requires an extensive system must be quite low. For example, if a minimum burrow length is required by a pocket gopher to have enough surface area for oxygen diffusion, then a short burrow might be insufficient, especially when coupled with the high oxygen demands of digging. The same would be true for male pocket gophers that must have burrows of certain lengths (and shapes) to obtain mates—a short burrow would be of little value (Reichman et al., 1982). If resources for subterranean mammals are uniformly distributed (and of approximately equal quality), then an individual starting a new burrow could expect to receive rewards proportional to the length of burrow excavated at any one time. If resource densities were high enough, then digging any particular distance would more than pay for the costs of the excavation. However, it is unlikely that resources are uniformly distributed (Andersen, 1982, 1987a; Andersen and MacMahon, 1981), so that an individual initiating a new burrow might have to “pay” by digging initially unrewarding burrow segments before encountering sufficiently rich patches to offset the initial excavation costs.

The investment in simple burrow systems may be so small that there would be little advantage to maintaining and passing them on to their offspring. Inhabitants of large, costly burrow systems, however, would benefit by evolving traits that would maximize the probability that their offspring would inherit the burrows and such investments as nests and
food caches. Jones (1984) showed that such patterns exist among bannertailed kangaroo rats, which build elaborate dens that may take 2 years to complete (Best, 1972).

3.2. Predation

Another disadvantage of a burrow is that the occupant's movement is limited while in the burrow. Snakes are known to enter burrow systems and consume adults or their young. For example, King (1955) and Halpin (1983) showed that snakes will enter prairie dog burrows and eat young pups. Brett (1990) observed a mole snake entering the burrow of a naked mole rat colony accompanied by loud noises coming from the colony. When the snake was captured it was found to contain several mole rats and excavation of the breached burrow system revealed an additional dead mole rat and extensive plugging by the remains of the colony. Knopf and Balph (1969) observed on several occasions a badger actually blocking the subsidiary exits to a Uinta ground squirrel (Spermophilus armatus) burrow before digging into the main entrance and extracting the adult and/or her young.

3.3. Sensory Deprivation

While below ground, mammals are buffered from many features of the above-ground environment, including contact with neighbors. Those species that come above ground often (e.g., every night) can still communicate with mates or competitors in typical ways (such as visual or chemical signaling), although alternative modalities may be used. For example, Kenagy (1976) describes a foot-drumming encounter between two kangaroo rats negotiating access to a mate. Randall and Stevens (1987) analyzed foot drumming by kangaroo rats in the presence of snake predators and concluded that it was a signal to let the potential predator know it had been detected. Randall (1984) describes the role of foot drumming in territorial defense and advertisement. Typical modes of communication such as vision and odor are probably ineffective for subterranean species, many of which have evolved alternative modes of communication. For example, Heth et al. (1987, 1988) and Nevo et al. (1987) reveal a pattern of seismic and sound communication by Spalax ehrenbergi in which the sender raps out a message on the burrow ceiling with its head. Recent investigations have also indicated that the bathyergid Georychus capensis uses foot drumming for sending various signals (Narins, Reichman, Jarvis, and Lewis, unpublished data). It is reasonable to imagine that a totally subterranean mammal may have evolved a seismic sensitivity for communication with neighbors and as a mechanism for the detection of approaching predators.
Mammals that spend virtually their entire lives underground have very little access to light, which serves as an important environmental cue to many animals. However, even totally subterranean species occasionally come to the surface and short exposures to light are known to trigger biological clocks in some animals (Menaker, 1971). Furthermore, other cues, such as slight seasonal changes in soil temperature as the seasons change or increased insect or plant root activity, may reveal important information to underground residents.

3.4. Dispersal

For animals that do not spend the vast majority of their lives in burrows, dispersal over the ground would be just like that for any nonburrowing mammal. For completely subterranean forms, however, dispersal becomes a problem. If the mammals disperse through the ground, the energetic costs could be staggering (Vleck, 1979). If they attempt to disperse above ground, they may find themselves in the unfamiliar role of walking or running on the surface. The consequences of such above-ground excursions are revealed in hundreds of reports of bones found in owl pellets, although it is not clear that subterranean species suffer any greater predation pressures during dispersal than typical surface mammals.

3.5. Burrow Environment

While it is reasonable to assume that living in burrows provides a net benefit to the inhabitants (see Section 2.4), there are a number of liabilities that can reduce the advantages of a below-ground habit. If water tables rise in the vicinity of burrows, burrows may have to be abandoned, as happens for some rodents in alpine meadows when the spring melt occurs (Howard and Childs, 1959). Under the worst of circumstances, mammals trapped in their burrows may drown.

Many mammals that live in burrows spend much of the day in the burrow, and specifically a nest within the burrow, and may inhabit that same system for months or years. The nests thus can become areas where parasites can rely on encountering a host. Thousands of articles in the medical and natural history literature detail the endoparasites and ectoparasites associated with burrowing mammals. It is sufficient here to note that all burrowing mammals no doubt host parasites, and specific features of their burrows and nests, such as the benign environmental conditions and constant host availability, may promote a particularly rich parasite fauna.

The environmental conditions that make burrows beneficial for mammals are also advantageous for an array of microbes. Even in deserts,
mammalian burrows exhibit moderate temperatures and are characterized by high humidities (e.g., Kay and Whitford, 1978). While very little is known about the microbial inhabitants of mammalian burrows, a few recent studies have revealed their importance for one group of mammals. Reichman et al. (1985) found over 30 species of fungi associated with the cheek pouches and burrows of kangaroo rats in southern Arizona. The conditions in kangaroo rat burrows are ideal for fungal growth and mycotoxin production (Reichman et al., 1985), which may lead to an array of beneficial and detrimental interactions between rodents, seeds, and storage fungi.

4. ADAPTATIONS FOR BURROWING

The underground environment is characterized by specific features that are absent from above-ground habitats. Thus, it is not surprising that fossorial mammals possess characteristics which are effective for constructing and inhabiting burrows. Many of the anatomical traits relate to burrowing activities while physiological adaptations tend to be related to living in the underground environment. Behavioral specializations involve both digging and living in burrows.

4.1. Morphological Adaptations

A glance at the forelimbs and claws of a mammal may be enough to reveal whether it burrows or not. In addition, the subterranean taxa show remarkable convergence in overall body plan and specific traits associated with digging (Nevo, 1979). As Hildebrand (1985) notes, morphological modifications of fossorial forms relate first to the need to loosen and transport a resistant material (soil). Specifically, this requires a digging implement, a capacity to produce and transmit a significant force, an ability to transport a load, and stamina for digging.

Fossorial mammals tend to exhibit digging specialization centered around either their teeth or their claws (Lessa and Thaele, unpublished manuscript). Those that specialize in tooth digging usually have large, strong, rapidly growing incisors that are deeply rooted and, in the case of some bathyergids, originate behind the cheek teeth (Hildebrand, 1985). Lower incisors are most often used to dislodge dirt (Hildebrand, 1985) and so they tend to wear faster than upper incisors or cheek teeth. Howard and Smith (1952) and Miller (1958) indicated that lower incisors in the pocket gopher Thomomys grow over 1 mm/day while upper incisors grow at about half this rate. It has been suggested that incisor growth rates vary with the hardness of soil the rodent inhabits (K. Davies, pers. commun.). It is not known whether differential growth rates of claws and teeth is a
facultative response or a genetic trait of populations adapted to local conditions. A number of totally subterranean forms can close their lips behind their teeth, precluding soil from getting into the mouth (Nevo, 1979; Hildebrand, 1985).

Many rodents also use their claws as well as their teeth for digging, and most moles and the larger fossorial mammals use their claws exclusively. Claws on digging mammals tend to be laterally compressed (Hildebrand, 1985) and a bony phalanx often extends into the claw. Forelimbs are most commonly used for excavation (although rear limbs are often used to kick loosened soil backward) and hence have rapidly growing claws that are modified for digging and grow quickly. Howard (1953) noted that the growth rate of pocket gopher nails varied between individuals and between digits and that the claws that are the most involved with digging grew the fastest. Moles, which often inhabit relatively friable soil, also use the digits and palms of their forefeet to push soil aside or move it backward.

Some mammals use their heads or noses to force their way into the soil. Moles, golden moles, Myospalax, and Spalax exhibit this digging pattern, and most have hardened pads covering the surfaces used for digging (Hildebrand, 1985).

The production of forces capable of dislodging soil requires large muscle masses, and the effective transmission of forces involves high power arm (in-lever) to load arm (out-lever) ratios. Fossorial mammals exhibit these traits to a significantly greater degree than their nondigging relatives. Hildebrand (1985) discusses several modes of digging (e.g., scratch digging, tooth digging, head elevation digging, etc.) and presents evidence that specializations associated with each mode are reflected in the skeletal and muscular arrangements in each taxon. Generally, there is an increase in muscle mass and volume (although not usually muscle length) in body parts used for the various types of digging. Furthermore, bones related to the digging modes tend to become broad and faceted, reflecting their function as platforms for the attachment of powerful muscles (Lehmann, 1963; Yalden, 1966). In all cases, measures of the degree of specialization for digging (e.g., the ratio of humeral width to length) are highest in those taxa that are fossorial compared to nonfossorial forms. Mechanical specializations which increase the power of the skeletal/muscular lever system are also found in active diggers. For example, the olecranon process (elbow) of armadillos extends well beyond the juncture with the humerus, magnifying the force exerted by the muscles of the upper forelimbs and back (Miles, 1941).

It is important for many of the specialized diggers to anchor parts of the body not directly involved with the movements of digging, thereby providing a stable platform for the transmission of force. For example, the shoulder must be stabilized to serve as a foundation for forelimb move-
ment, and most of the fossorial mammals possess either specific adaptations for such stabilization or enhancements of traits found in their less specialized relatives (Puttick and Jarvis, 1977). In addition, joints must be strengthened against dislocation caused by the powerful strokes of the various digging motions. A number of general modifications are seen in fossorial forms to accomplish these ends. For example, in powerful diggers there is a tendency for joint motion to become limited to one plane, joints to become strengthened against lateral movement, and the fusion of skeletal elements, all of which reduce extraneous movement (Hildebrand, 1985).

Just as the specific joints involved in digging must be stabilized, the entire platform (i.e., the body) must also be anchored in a way that promotes efficient transfer of forces to the digging effort. In large diggers such as aardvarks, pangolins, etc., the weight of the body may be enough to counter the forces produced by digging. Smaller mammals usually brace themselves with their rear claws and hindlimbs, and this generates modifications in the structure of the pelvis (Hildebrand, 1985). There tends to be fusion of sacral elements, and bone reductions or elaborations in the pelvis which reflect specific muscular attachments.

Movement within the burrows and the transport of soil also yield modifications in fossorial mammals: Species that are entirely subterranean usually construct tunnels that are only slightly larger than their own diameter (Andersen, 1982). When individuals turn around in the burrow, they seem to almost turn inside out as they hunch over, push their head between their rear legs or under their forearm, rotate half a spin, and emerge pointing in the opposite direction. This movement is enhanced by loose skin (Tucker, 1981) and hair that either slopes away from the direction of movement or occurs as short, easily bent bristles (Nevo, 1979; Tucker, 1981).

Several taxa of fossorial mammals have expanded internal cheek pouches (e.g., many squirrel species) and the heteromyids and geomyids, which are closely related, possess large external cheek pouches in which they carry various items, especially food (Reichman, 1975; Morton et al., 1980; Nikolai and Bramble, 1983). Cheek pouches also occur in nonburrowing mammals (e.g., tree squirrels) and appear to be associated with gathering food and bring it back to a central location rather than burrowing per se (see Section 4.3 for a discussion of caching behavior).

Some of the senses in fossorial mammals are reduced, especially in those that are entirely subterranean. For example, virtually all of the subterranean forms have relatively small eyes. Further, the bathyergids are apparently blind, even though they possess external eyes, and the eyes of the marsupial mole, the chrysochlorids, Spalax, and some Talpa species are completely covered by skin (Nevo, 1979). Golden moles have an enlarged malleus–incus complex whose function is unknown. Because the
soil is such a dense medium, it is reasonable to suspect that fossorial forms may have increased sensitivity to low-frequency sounds (R. Hefnner, pers. commun.). Furthermore, recent investigations revealed that Spalax (Heth et al., 1987, 1988) and the bathyergid Georychus (Narins, Reichman, Jarvis, and Lewis, unpublished data) are sensitive to seismic vibrations.

The tactile sense seems especially well developed in fossorial forms, many of which have sensitive hairs over all their body (Quilliam, 1966; Nevo, 1979; Hildebrand, 1985). Some species also have sensitive vibrissae; Dubost (1968) and Armstrong and Quilliam (1961) detailed the thousands of sensory papillae in the noses of moles which are innervated by 15–20 nerves each.

While many fossorial mammals possess fur typical of generalized mammals, the subterranean taxa tend to have thin or silky hair, perhaps related to the problems of shedding heat loads (McNab, 1966, 1979). The extreme form of sparse fur occurs in Heterocephalus, the naked mole rat, which has only a few long hairs on its body. Many that do have fur tend to match the color of the background soil they inhabit (Benson, 1933; Ingles, 1950; Getz, 1957; Patton, 1973). Piebald patterns occur occasionally in some pocket gopher populations. It is unclear why the patterns occur; Hafner and Hafner (1987) propose that in populations they studied the pattern was an incidental phenomenon with no adaptive significance. Virtually all members of the bathyergid Georychus capensis have white patches, which is especially peculiar because the pattern is not restricted to a few isolated populations and all members of the species are blind. Cryptomys hottentotus, another blind bathyergid, exhibits a color dimorphism (dark brown and a light grayish brown) that is independent of the sex or age of the colony member (N. Bennett, pers. commun.).

4.2. Physiological Adaptations

The physiological adaptations that characterize fossorial mammals revolve around managing heat production and dealing with peculiar gas relationships (i.e., hypoxia and hypercapnia) within the burrow (McNab, 1966, 1979; Nevo, 1979; Hildebrand, 1985). The degree of specialized responses to these phenomena appears to be highly correlated with the amount of time members of a taxon spend underground.

While the soil insulates burrow inhabitants from the extremes of the above-ground environment, it also reduces the ability of the animals to shed a heat load built up during normal metabolic activities or hyperactivity associated with digging. Burrows also tend to possess high relative humidities, so that evaporative cooling from respiratory surfaces or from licking the skin and fur is inefficient in burrows, further exacerbating the heat-loss problem. This is much less of a concern for those mammals that
spend a portion of the day outside the burrow where normal processes (radiation and convective cooling) can help them dump excess heat generated by increased activity. Mammals that are completely subterranean have evolved several traits that reduce the problem of getting rid of excess heat. One primary response is a significantly reduced metabolic rate and body temperature, which reduces the amount of heat produced by the animal, and McNab (1966, 1979) has found this to be the case for species weighing more than 80 g. Concurrent with reduced metabolism is an increase in thermal conductance via skin vascularization and reduced pelage thickness. Indeed, McNab (1966) showed that the pocket gopher Geomys loses 30% of its body heat through its tail. Some authors have suggested that reductions in body size may be an adaptation to cast off excess heat, but Patton and Brylski (1987) show that variation in body size is environmentally mediated in some pocket gopher populations. While the association of reduced body size and heat loss is suggestive, it is difficult to prove that heat dumping is the primary selective force promoting smaller size.

The extreme manifestation of traits that may be associated with heat dumping is the naked mole rat, which is small, virtually hairless, possesses a basal metabolic rate 40% below what would be predicted for its weight, and has the poorest ability to thermoregulate of any mammal tested so far (McNab, 1966). Such traits also make mole rats more susceptible to low temperatures, even though the low temperatures in burrows tend to be quite moderate compared to above-ground air temperatures. To overcome the effects of low temperature, naked mole rats tend to huddle together, reducing the costs to individuals of maintaining their body temperature (Withers and Jarvis, 1980). While these traits may reduce the problem of heat load, Jarvis (1978) suggested that the prime selective force for the reduced metabolism seen in naked mole rats is the extremely reduced resource levels found where they occur. Lovegrove (1986, 1987) suggested a similar origin for the low metabolic rates of Georychus capensis, Bathyergus janetta, and the largest bathyergid, B. suillus. The extreme combination of traits seen in the naked mole rat may be responsible for “allowing” it to live in hot, dry areas of eastern Africa, but may also restrict it to the equatorial regions where low temperatures are not a significant factor.

A second suite of physiological traits in fossorial mammals is related to the low oxygen and high carbon dioxide levels that can occur in burrows, especially those that are sealed (see Section 2.4). Nevo (1979) summarizes several physiological traits associated with gas transport and blood properties that promote tolerance of hypoxia and hypercapnia in fossorial mammals (Table II). As expected, the completely subterranean taxa exhibit the most pronounced physiological adaptations to the below-ground atmosphere (see Ar et al., 1977; Arieli and Ar, 1981a,b; Arieli et
TABLE II
Some Physiological Adaptations of Fossorial Mammals to the Environments of their Burrows

<table>
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<th>Traits</th>
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<th>Subterranean insectives</th>
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<tr>
<td>Thermal conductance</td>
<td>High</td>
<td>?</td>
</tr>
<tr>
<td>Thermoregulatory ability</td>
<td>Low</td>
<td>?</td>
</tr>
<tr>
<td>Body size</td>
<td>Dependent on temperature and resource availability</td>
<td>Small</td>
</tr>
</tbody>
</table>

**Blood gas properties**

<table>
<thead>
<tr>
<th>Trait</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low respiratory rate</td>
<td>Increased ventilation during hypercapnia</td>
</tr>
<tr>
<td>Low response threshold to hypoxia</td>
<td>Heart resistant to respiratory acidosis</td>
</tr>
<tr>
<td>Low and arrhythmic heart rate</td>
<td>High O\textsubscript{2} affinity of blood</td>
</tr>
<tr>
<td>High erythrocyte count</td>
<td>Low acid-base regulatory ability</td>
</tr>
<tr>
<td>Low corpuscular volume</td>
<td>High muscular hemoglobin content</td>
</tr>
<tr>
<td>Wide dissociation curve for O\textsubscript{2}</td>
<td></td>
</tr>
<tr>
<td>Modified hemoglobin</td>
<td></td>
</tr>
<tr>
<td>Tissue function at low PO\textsubscript{2} and high PCO\textsubscript{2}</td>
<td></td>
</tr>
</tbody>
</table>

*Not all fossorial mammals possess all of these traits.
Source: Data are from Nevo (1979) and citations therein.

al., 1984, for a thorough analysis of Spalax), but other forms show similar trends. For example, Faleschini and Whitten (1975) showed that among three species of sciurids, the species that are most fossorial exhibited the greatest tolerance to hypoxia. Hall (1965) found a direct relationship between oxygen affinities of hemoglobin and the degree of burrow use in seven sciurid species from prairie dogs to flying squirrels. MacLean (1978) found that even the semifossorial Tamias exhibited a greater tolerance of hypercapnia than nonfossorial relatives. Withers (1977), however, observed that the CO\textsubscript{2} sensitivity of the semifossorial pocket mouse, Perognathus longimembris, was similar to nonburrowing small mammals. Similar results have been obtained for a variety of burrowing mammals including echidnas (Augee et al., 1971; Hochachka et al., 1984), shrews and moles (Bartels et al., 1969), armadillos (Kay, 1979), pocket gophers (Chapman and Bennett, 1975; Darden, 1972), and kangaroo rats (Soholt et al., 1973).

Several of the physiological adaptations observed in fossorial mammals complement each other. For example, a reduced metabolic rate decreases heat production and also reduces the amount of oxygen consumed and CO\textsubscript{2} produced. Reduced metabolic rates also decrease water loss (on most diets) while the high moisture content of the burrow atmosphere minimizes evaporative water loss.
Jarvis and her coworkers are just beginning to analyze an intriguing physiological trait that appears to be related indirectly to the totally fos-orial existence of the naked mole rat. They are discovering that pheromones and/or hormones associated with a common toilet area in the communal burrows of Heterocephalus seem to allow the single breeding female in a colony (Jarvis, 1990) to prevent any reproductive cycling by other females. While details are sketchy at this time, the use of common toilet areas seems to be correlated with changes in sex hormones in colony members (see Jarvis, 1990 and Sherman et al., 1990). Such a system may not be unique to the naked mole rat, but this species does appear to exhibit the most elaborate social and hormonal interactions among fos-sorial mammals.

Many mammals use torpor and hibernation as strategies for avoiding the environmental extremes. A major feature of these tactics involves drastically lowering metabolic functions, which has the effect of reducing the imbalance of oxygen and CO₂ in the burrow. Nevertheless, the atmosphere in burrows of torpid and hibernating mammals can become quite atypical of the above-ground atmosphere (Williams and Rausch, 1973). Few mammals have been adequately studied under such conditions, but what few have indicate that they can endure incredible concentrations of CO₂ and depletion of oxygen (Williams and Rausch, 1973; MacLean, 1981).

4.3. Behavioral Adaptations

4.3.1. Digging

The most obvious behavior associated with fos-sorial mammals is the actual act of digging (see Hickman, 1984b for an extensive analysis of the digging behavior of geomyids). Some taxa may or may not excavate burrows, depending on their local environment. For example, most beavers construct stick and log houses in ponds produced by dams the rodents build. In rivers which are too large to dam, however, the beavers excavate burrows in the riverbanks (Ognev, 1947). Shump and Christian (1978) analyzed the digging behavior of Sigmodon hispidus and discovered that populations in Florida were much more likely to dig burrows than cotton rats from Kansas. Laboratory studies indicated that the difference was due to soil characteristics; sandy soils in Florida promoted digging while the hard soils in Kansas inhibited burrowing behavior.

Moles and golden moles simply push soil aside while excavating their shallow surface runs, which usually generates a low ridge on the surface just above their tunnels. Most fos-sorial mammals loosen dirt with the claws on the forefeet, scoop it under them, and kick it out behind. This simple procedure suffices for species excavating relatively shallow bur-
rows. Those species that dig longer burrow segments must haul the loosened soil to an exit or to an abandoned tunnel. In the former case, many obvious mounds are produced on the surface while in the latter the subterranean activities are not obvious on the surface. Vleck (1979) hypothesized that there should be an optimum distance between lateral openings to the surface for the deposition of soil. Studying pocket gophers (Thomomys), he calculated what this distance should be in specific soil types. He then excavated a number of burrows and measured the average distance between the “lateral”s and discovered that most were separated by a distance that minimized the costs of hauling dirt above ground.

Most subterranean species move dirt to its deposition site by reversing in their burrows, forming a broad surface with their forelimbs and chest, and pushing (Hickman, 1984a). Bathyergids and ctenomyids remain facing away from the excavated dirt and kick it rearward toward the deposition site (Hickman, 1985). The most striking excavation behavior occurs in the naked mole rats, which form chains of diggers (Jarvis and Sale, 1971). The individual first in line loosens some soil and works his way backward with the soil. As he moves, those behind straddle him and move forward, eventually taking up their position at the head of the line. Once an opening is reached, the carrier drops the load and a designated individual kicks the dirt up and out, producing a volcano-like eruption on the surface (Brett, 1990). Many burrowers tamp the dirt with fast thrusts of their forefeet as they deposit it above ground. The purpose of this behavior is not known, but it may be to harden the soil against a potential intruder or to reduce the amount of space needed for the excavated soil.

Reichman et al. (1982) discussed the adaptive geometry of pocket gopher burrows and noted that on a number of occasions when breaks were made in the burrow system of an individual pocket gopher the disconnected ends of the burrows would be reunited the next day. There were virtually no loops in these burrow systems, so the individuals were isolated in one end of the system when it was bisected. Nevertheless, the pocket gophers seemed to have the ability to reconnect the two segments. This same ability has been noted in bathyergids, leading Eloff (1951) to attribute special orientation skills to these animals.

4.3.2. Individual Interactions

While some taxa of fossorial mammals are colonial, the majority are solitary, except when they share a burrow with a mate or offspring. Most of the noncolonial, totally subterranean rodents are highly aggressive toward one another (Hickman, 1973, 1977b; Gregory et al., 1987). Hansen and Miller (1959) present data for plural occupancy of pocket gopher burrows and note that it is more common in June and July when courtship and breeding may be occurring. The authors also indicate that female/
young combinations are the most common while male/female, female/female, and male/male combinations are rare. Reichman et al. (1982) found several cases of deep, shared nests between male and female Thomomys bottae. Some of the nests contained young and the path from the male's burrow to the nest was well worn, suggesting some form of paternal care, an unusual phenomenon in mammals. Very little is known about parental care or about courtship and mating in strictly subterranean species. Bennett and Jarvis (1988) discuss the breeding behavior in Georychus capensis and Jarvis (1990) gives an overview of bathyergid reproductive behavior.

4.3.3. Activity

The activity patterns of mammals that are not strictly subterranean are related more to their needs outside the burrow than to what occurs within the burrow. Thus, most digging mammals are nocturnal and may adjust their activity to particular environmental conditions such as temperature, weather, and moonlight. Totally subterranean taxa are less influenced by a circadian cycle and thus frequently show activity patterns that are not associated with the day/night cycle. For example, Gettinger (1984) noted that Thomomys spend about 15 h/day in their nests. Activity was spread throughout the remainder of the day, although it was significantly concentrated between 1600 and 2000 h. Conversely, Cameron et al. (1988) found no periodicity in daily activity in the pocket gopher Geomys attwateri. Jarvis (1973) found a marked contrast in the activity patterns of two subterranean rodent species, with Tachyoryctes showing a distinct peak in activity between 1000 and 1900 h while Heliophobius was active over more of the day (while still showing a slight peak in activity around the same time as Tachyoryctes). The author noted that Tachyoryctes can see light and occasionally comes to the surface to forage, which may set its circadian cycle, while the other species is blind and rarely comes to the surface. Harvey (1976) found eastern moles (Scapanus aquaticus) active throughout the day, with peak activity periods tending to occur from 0800 h to 1600 h and from 2300 h to 0400 h. The moles stayed in their nests for an average of over 3 h at a time and their foraging bouts lasted almost 5½ h at a time.

As with daily activity, the yearly activity pattern of mammals that are not strictly subterranean are determined primarily by conditions outside the burrow. Thus, animals may be active in spring and fall, exhibit a somewhat reduced activity in the heat of summer, and remain in their burrows longer in the winter when conditions are harsh or food is limited, perhaps descending into torpor or hibernation (e.g., Reichman and Van De Graaff, 1973; Reichman and Brown, 1979). Completely subterranean species usually stay active throughout the year. For example, pocket
gophers continue to excavate burrows in areas where snow covers the ground. Presumably because it is difficult to construct the typical mounds when snow is on the ground, pocket gophers dig short, branched tunnels in the snow in which they deposit the residue of their winter excavations. These tailings remain as dense plugs of soil on the surface after the snow melts in spring.

Early studies of pocket gopher activity cycles used the production of new mounds as an indication of activity (Miller, 1948; Laycock, 1957). This can give spurious results, however, as some pocket gophers fill abandoned burrows with dirt from fresh excavations, leaving no indication on the surface of underground activity. Nevertheless, mound counts and other techniques indicate that strictly subterranean species are most active when the soil is moist, which often coincides with peaks in resource production (e.g., vegetation, insects) and is also when the soil is most friable.

4.3.4. Foraging

The foraging behavior of many burrowing mammals is probably similar to that of their nonburrowing relatives. Very little is known, however, about how subterranean taxa acquire food because of the difficulty in observing them in the soil. It is reasonable to imagine that as these mammals dig through the soil they encounter an array of food types (invertebrates, plant parts), accepting or rejecting them on the basis of their particular dietary specializations (i.e., insectivore, herbivore). It has been suggested that subterranean foragers probably take anything that is not toxic because of the high costs associated with their burrowing activity precludes them from being selective (Nevo, 1979; Du Toit et al., 1985; Lovegrove, 1987).

While subterranean herbivores may simply clip off below-ground plant parts and either consume them or store them, many investigators have observed whole plants being pulled below ground. Vaughan (1966) noted that when pocket gophers recovered a plant root, they rapidly vibrated it with their forefeet and teeth, presumably to dislodge dirt that would prematurely erode their teeth.

4.3.5. Caching

Many burrowing mammals cache food in their dens. The amount of food stored and the length of time the occupant relies on the cache varies considerably from a day or two to several months (Smith and Reichman, 1984). Some species store huge quantities of food. For example, Lovegrove and Jarvis (1986) found 4944 bulbs, corms, and tubers in the burrow of Georychus capensis and 537 corms and bulbs in the burrow of a colony
of Cryptomys hottentotus. Vorhies and Taylor (1922) report hundreds of thousands of seeds in the caches of banner-tailed kangaroo rats. Even insectivores store their prey, occasionally immobilizing them with mild venom or disabling them so that they can't crawl away before being consumed (Smith and Reichman, 1984).

Caching behavior might be expected to vary within a species based on such features as the availability of resources, the severity of winter, and the presence of competitors (Sanchez and Reichman, 1987). Reichman and Fay (1983) found, as hypothesized, that a caching species of rodent had a more diverse diet when feeding from a cache than a noncaching species. The proposed explanation was that a caching species has more control over its food than an animal foraging above ground every night in the presence of competitors and thus could have a diverse diet without a high probability of losing valuable food items to a competitor.

As noted earlier, the below-ground environment hosts many microbes and fungi which can cause stored food to spoil. Some heteromyid rodents that cache large quantities of seeds appear to prefer slightly moldy seeds (Rebar and Reichman, 1983; Reichman and Rebar, 1985; but see Frank, 1988). Furthermore, Reichman et al. (1986) showed that under laboratory conditions mimicking those in the field, banner-tailed kangaroo rats can "manage" stored seeds to promote mold growth on sterilized seeds and inhibit further mold growth on seeds molded to a level they are known to prefer. The molds involved in this system are ubiquitous soil fungi which the rodents cannot avoid, but there is reason to believe that they have evolved mold detection mechanisms and management procedures which minimize the liabilities and maximize the benefits of the stored seed-fungus relationship.

4.3.6. Predator Avoidance

One of the major advantages of burrows is the protection they offer against predators. Many burrowing mammals that spend time above ground feeding and interacting with conspecifics scurry back to their burrows when alerted to the presence of an unusual intruder. Even subterranean species such as pocket gophers tend to retreat to their relatively deep nests when something approaches aboveground (K. Zinnell, pers. commun.). As noted earlier, however, burrows can also become traps in which mammals can be cornered. To minimize the risk of detection and capture in their burrows (among other reasons), many mammals seal their burrow entrances while inside. Of course, subterranean mammals keep their burrows sealed virtually all the time. Burrow inhabitants will wall off segments of their burrows invaded by predators, and Brett (1990) describes a furious encounter between a mole snake and naked mole rats (see also Section 3.2).
BURROWING MAMMALS

Some burrowing mammals foot-drum in the presence of a predator (Randall and Stevens, 1986). A similar behavior has been observed and recorded for the bathyergid Georychus capensis, in which foot drumming directed toward an intruder appears different from the signal used during what was taken to be courtship (Narins, Reichman, Jarvis, and Lewis, unpublished data). Another species of bathyergid (Cryptomys hottentotus) displays a peculiar body-pumping behavior in the presence of distractions that it may take for a predator (Eloff, 1951; N. Bennett, pers. commun.). An individual in a colony will face down a tunnel toward the presumed intruder and pump rhythmically with a wavelike movement of the body from head to tail (De Graaff, 1964 and observations by O.J. Reichman in a laboratory setting). The purpose of the behavior is not known, but it may be to draw odors of the intruder toward the colony defender.

4.3.7. Territoriality

Presumably, most burrowing mammals act out their territorial interactions with the same variety of behaviors (such as scent marking, aggression, display) as nonburrowing mammals. Subterranean taxa, however, probably have their repertoire limited by an environment that is relatively opaque to behavioral and sensory interaction. Thus, it has been postulated that sound or seismic communication may be an important element of their behavior (Nevo et al., 1987). Interestingly, the few studies of subterranean forms indicate that individuals (or colonies) are highly aggressive toward each other. For example, Hickman (1977a) describes the aggressive interactions between several geomyid species, and Gregory et al. (1987) found that male/male, female/female, and male/female combinations were equally aggressive toward each other. One of us (O.J.R.) observed the courtship interactions between several pairs of G. capensis, which are often characterized by aggression for several days before courtship begins (also see Bennett and Jarvis, 1988).

5. INTERACTIONS WITHIN AND BETWEEN BURROW SYSTEMS

5.1. Interactions within Burrows

The most common interaction within mammal burrows is probably between females and offspring (Hansen and Miller, 1959). Not surprisingly, very little is known about such interactions but there is no clear reason to suspect that such activities as birth and nursing are significantly different between fossorial and nonburrowing mammals (although there do not seem to be any primarily subterranean taxa which have precocial young). It would be advantageous for mammals that invest heavily in their nests
or dens to evolve mechanisms to ensure that their own offspring inherit the structure, and burrows would certainly fit into this category. Jones (1984) analyzed the inheritance patterns of kangaroo rat burrows and noted that offspring often stay in the natal burrow well beyond the age of weaning and many take over their mothers' burrows. Furthermore, 70% of the offspring end up with their mothers' dens or just one burrow system away from their natal burrows. King (1955) noted that female prairie dogs occasionally give up their burrows to their offspring and move to new quarters themselves. We do not know of any such patterns of inheritance among the subterranean taxa, although they would seem to be prime candidates for such a pattern.

A variety of mammals are known to cluster or huddle in burrows, especially in inclement weather or cold seasons. Of course, social species from prairie dogs to naked mole rats take advantage of group living, but even some species that are normally solitary will congregate during certain seasons. For example, Morton (1978) describes congregations of the dasyurid Smilhopsis crassicaudata that vary in size and constitution. The selective forces that promote colonial existence include resource abundance and distribution, predator avoidance, and degree of relatedness (see Sherman et al., 1990).

As with other mammals, a significant amount of time is spent grooming and in those species that are colonial, members may groom each other (Jarvis, 1990). Newborn naked mole rats beg feces from older individuals in the colony, which feed their own pellets to the young (Jarvis, 1986b). While one function of this behavior might be to inoculate the gut of the young with microbes, the behavior continues for many weeks, beyond that which would seem necessary for simple inoculation. This suggests some additional, unknown function for this behavior.

5.2. Interactions between Occupants of Different Burrow Systems

Many mammals construct their burrows at the base of some structure such as a tree, shrub, or rock. Thus, it is possible that burrow sites may be limited in areas where such structures are necessary and uncommon (Merriam, 1971). This is probably not the case in most habitats, however, so burrow spacing may reflect underlying territories based on some other resource such as food. Schroeder and Geluso (1975) analyzed the spatial distribution of occupied and unoccupied kangaroo rat burrows and found that they were uniformly distributed. The authors suggest that the regularity of the burrow spacing indicates that Dipodomys spectabilis minimizes intraspecific interactions by spatial means.

Spacing is especially critical for subterranean taxa for whom the burrows are the resource (providing access to food, mates, etc.). Thus, the burrow configuration themselves reveal the relationship between the resi-
dent and the resources. Reichman et al. (1982) describe an underlying geometry of the spacing and configuration of the burrows of two populations of pocket gophers. They noted that to compensate for a twofold decrease in plant production, individuals in one of the populations doubled their average burrow length while maintaining statistically indistinguishable spacing values. However, neither Andersen (1987a) nor Cameron et al. (1988) detected any relationship between burrow geometry and resource distribution.

It is extremely unusual for two or more species of subterranean herbivores to be sympatric over broad geographic areas. For example, Thaeler (1968) noted that at several boundaries between populations of two species of pocket gophers, the burrows of the two species interdigitated for just a few meters before giving way to monospecific distributions. Reichman and Baker (1972) found a similar narrow band of overlap between the geomyids Pappogeomys castanops and Thomomys bottae. Pappogeomys castanops, the larger, more xeric-adapted species (Judd and Reichman, 1972) was gradually replacing the smaller species (Reichman and Baker, 1972; Williams and Baker, 1976). While the subterranean habitat may appear to be three-dimensional, with depth added to the two dimensions of a surface habitat, the depth component is quite narrow because of the distribution of resources. For example, it would presumably be advantageous for subterranean herbivores to focus their foraging efforts within the concentrated root zone. However, this zone is relatively shallow, greatly reducing the width of the third dimension (Soriguer and Amat, 1980). One of the few places in the world where more than one species of subterranean mammal overlap over broad areas is in the western Cape Province of South Africa. There, three closely related genera of bathyergids overlap and display some degree of vertical stratification (Davies and Jarvis, 1986; Lovegrove and Jarvis, 1986). Reichman and Jarvis (1989) analyzed the use of plants by these populations and discussed the ecological means by which this subdivision may take place.

As expected, there is no such problem with subdividing an area between subterranean insectivores and herbivores. McConnell (1986) discovered no behavioral or ecological interactions between an insectivorous golden mole (Amblysomus) and a herbivorous mole rat (Cryptomys hottentotus) and Scheffer (1945) often caught subterranean insectivores (moles) and herbivores (pocket gophers) in the same area.

5.3. Burrow Cohabitants

The microbial cohabitants in rodent burrows were discussed in Section 4.3. Burrows may also house a variety of vectors that carry several major diseases. For example, phlebotomine sand flies carry the protozoa that causes leishmaniasis and rodent burrows appear to be a reservoir for
the flies, and hence the disease, in several parts of the world (Dubrovsky, 1975; Chippaux and Pajot, 1983). In other cases, mammals that live in burrows host vectors (e.g., fleas that carry bubonic plague; Longanecker and Burroughs, 1952; Lechleitner et al., 1962) but it is not clear that burrowing per se has a direct role in the relationship. At the very least, the burrows probably provide a moderate environment for the vectors and as foci for their dispersal onto other individuals (Morozov and Rapoport, 1983; English abstract only).

Mollusks can be found in rodent burrows (Baumann and Jungbluth, 1979) and arthropods are very common. The Russian literature is especially rich in research that indicates several tropic levels and over 250 species of invertebrates in gerbil burrows (Krivokhatskiy, 1982a,b; English abstract only). Similar studies exist for pocket gophers (e.g., Hubbell and Goff, 1940), prairie dogs (Sheets et al., 1971), and voles (Haitlinger, 1983). Burrows often host communities of invertebrates, with some feeding on vegetation, fungi, or the mammalian hosts, and these taxa being consumed by predators (Seastedt et al., 1986). Seastedt et al. (1986), in an analysis of the microarthropods and nematodes of kangaroo rat burrows, could find no difference in the invertebrate fauna of occupied and unoccupied burrows, although the high variation in the data from different burrows may have obscured broader patterns.

Scheffer (1945) found voles, deer mice, shrews, house mice, ground squirrels, weasels, and bull snakes in mole burrows. Obviously, several of these were predators and not true cohabitants. Vaughan (1961) found 22 species of vertebrates in pocket gopher burrows, including salamanders, toads, turtles, lizards, snakes, moles, rabbits, ground squirrels, and other small mammals. Campbell and Clark (1981) list 22 species of mammals, 33 bird species, five reptile species, and four amphibian species from prairie dog colonies. Ognev (1947) describes wheatears living in mammal burrows and burrowing owls are common residents of some prairie dog burrows (Martin, 1983).

6. IMPACT OF MAMMAL BURROWS ON THE ENVIRONMENT

Mammals living in burrows directly affect their environment by consuming vegetation or other animals, but these traits are not related to burrowing per se. For example, prairie dogs denude the areas around their burrows of vegetation, but nonburrowing, grazing mammals can do the same. An opposite pattern can also occur, as when woodchucks defecate near their burrow openings, enhancing plant growth (Merriam and Merriam, 1965).

More pertinent to this discussion are the ways in which the burrows and burrowing behavior affect the environment. The most immediate and
potentially extensive impacts of mammals burrowing are mediated through the deposition of tailings from the burrows. Except for subterranean species which deposit soil from new excavations in old burrows, all of the 'dirt' from burrows must be deposited on the surface. The most obvious effect is the smothering of plants covered by the soil. While we could find no data on the subject, it seems plausible that plant species growing from rhizomes or underground storage organs would have a greater opportunity to overcome an initial setback than other species, and so these types of storage structures might be selectively favored where burrowing mammals occur in significant densities.

While the mounds smother plants, they also serve as ideal germination sites in crowded habitats. Platt (1979) has documented the importance of badger mounds on prairies where germination sites are in short supply. Reichman (1988) found that mortality was high for an annual species (Berteroa incana) on pocket gopher mounds but that the survivors grew larger and produced many more seeds than individuals off the mounds. Andersen (1987b) reviewed below-ground herbivory and his presentation includes many articles that discuss the effect of tailings on vegetation.

Over the long term, perhaps the most important feature of burrowing is soil formation (Ellison, 1946; Andersen and MacMahon, 1985) and soil mixing (Kalisz and Stone, 1984). After soil is brought to the surface by burrowing activities, it erodes and redistributes nutrients. Inouye et al. (1987) found that in a very sandy area the soil that was brought to the surface by pocket gophers contained significantly less nitrogen than the surface soil and Reichman (1988), working in the same area, noted that soil used by pocket gophers to plug empty burrows contained less nitrogen than surrounding soil. The mounds and ridges generated by fossorial mammals also produce distinctive soil moisture profiles (Skoczen et al., 1976) which in turn probably affect plant success.

The presence of burrows themselves also impinge on plant success. Reichman and Smith (1985) found that plant biomass was reduced 25–50% over active pocket gopher burrows and that the effect was still detectable 3 years after the burrows had been abandoned. A similar impact has been noted over the burrows of three sympatric bathyergids (Reichman and Jarvis, 1989).

Some impacts of burrowing that appear minor in the short term accumulate to generate substantial long-term effects. For example, the extensive mounds produced by large species of kangaroo rats dramatically affect the vegetation that grows around and on them (pers. obs.). Even more dramatic are the large mima mounds which occur worldwide, apparently in relation to the burrowing activities of subterranean mammals. Cox and coauthors (Cox, 1984; Cox and Gakahu, 1983, 1985; Cox and Roig, 1986; Cox et al., 1987) analyzed the Dalquist—Scheffer hypothesis
that these large (5–20 m in diameter) mounds are apparently formed by the gradual movement of shallow soil toward a central location. This site attracts even more burrowing activity as the soil depth increases and plant succession produces food for the burrowing mammal. Eventually, a self-perpetuating pattern of disturbance ensures the persistence of the mound.

While soil mixing might be considered beneficial in the sense of promoting nutrient cycling, recent studies have revealed that mammal burrows near radioactive waste sites may promote the spread of deleterious radioactive material. Deer mice, kangaroo rats, voles, ground squirrels, and rabbits have been implicated in this phenomenon (O'Farrell and Gilbert, 1975; Arthur and Markham, 1983; Reynolds and Launde, 1986). Another interesting intervention on the part of fossorial mammals occurs where burrowers dig into, disturb, and redistribute archaeological artifacts (C. Adams, pers. commun.).

7. CONCLUDING REMARKS

We had initially imagined developing generalizations about what types of mammals construct burrows and under what conditions (Best, 1982). The behavior is so widespread, both taxonomically and geographically, that most generalizations are trivial. Basically, relatively small mammals make burrows (the largest being aardvarks, pangolins, giant armadillos, and some canids). Some taxa (insectivores and especially rodents) are heavily represented by fossorial forms and a few families of mammals are composed entirely of burrowing forms. The anatomical, physiological, and behavioral convergence of these specialists is impressive.

While there are some soils that are so hard that burrowing mammals probably cannot dig in them, fossorial forms do occur in some extremely indurate soils (e.g., naked mole rats). Burrows even occur in very wet areas where entrances or portions of the tunnels may be under water (e.g., water shrews and moles, beavers). Burrows may be more common at higher latitudes, where environmental conditions make burrowing a prudent behavior, but the paucity of data makes such analyses premature.

There does seem to be a relationship between how reliant a mammal is on its burrow and the complexity of the burrow system. Simple burrows seem to be constructed by those mammals that use their burrows primarily for shelter and perhaps to raise their young. As burrows take on extra functions, such as food storage, they become somewhat more complex. Finally, the subterranean taxa, which secure virtually all of their needs below ground, build the most elaborate burrows.

Mammalologists and ecologists interested in burrows and burrowing behavior have, for obvious reasons, concentrated on the taxa that are most
specialized for this habit. Information of the burrowing habits of mammals that construct relatively simple burrows tends to be part of the anecdotal literature, although some studies exist that deal specifically with simple burrows. Both types of studies are difficult but necessary if we are to learn about how mammals use the below-ground habitat and what effect they have on others organisms in the same realm.

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