



## A review of burrowing by semi-fossorial vertebrates in arid environments

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Ecological data bases were searched for citations dealing with burrows, burrowing vertebrates, and the environmental impacts of this phenomenon. Results from this partial search were divided into categories with artificial boundaries depending on the primary focus of the cited paper. These categories were natural history, ecological theory, and the disciplines of geomorphology, pedology, plant ecology, and animal community ecology. Suggested research topics are presented as well as a simple conceptual model of the role of the burrow in the environment.

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### Introduction

Arid regions occupy over one-third of the earth's land surface; in these regions potential evapo-transpiration greatly exceeds precipitation during most of the year (Buol *et al.*, 1997). Vertebrates have evolved physiological, morphological, and behavioral adaptations to cope with this aridity. Although animals burrow in other eco-regions, the possession of a cool, moist burrow with stable temperatures underground is especially critical for survival in arid zones that are hot and dry with greatly fluctuating temperatures on the surface. The burrowing trait in vertebrates evolved as early as the Carboniferous (Olsen & Bolles, 1975) and may have been responsible for the success of many early life-forms of the animal kingdom; certainly this represented the first type of 'shelter'. Moreover, the trait can be found across taxonomic and community boundaries worldwide. The resulting burrows vary greatly in diameter, depth, and complexity; they impact geomorphology, hydrology, soil dynamics, vegetation patterns, and animal community diversity at scales ranging from microsites to landscapes.

Burrowing is just one of a series of activities such as trampling, wallowing, digging, and geophagy that can have tremendous impacts on the landscape (see recent review by Butler, 1995; also Taylor, 1935; Jacob, 1940; Thorp, 1941; Abaturov, 1972; Hole, 1981; Meadows & Meadows 1991; Stone & Comerford, 1994). For these reasons, this

phenomena deserves study in its own right. This paper deals with burrows open to the surface dug by semi-fossorial vertebrates. The intent of this review is to present an overview of the rich variety of research conducted on vertebrate burrows; the paper is not intended as a comprehensive research agenda for the future.

## Methods

Data bases (Biological Abstracts, Agricola, Zoological Record, Wildlife and Fisheries Abstracts) were searched for journal articles, books, dissertations, and theses related to burrowing and the impact of burrowing. The paper is divided into highly artificial divisions, depending on the primary focus of the paper reviewed; these divisions are not mutually exclusive. The topics are (1) natural history, (2) ecological theory, and (3) the traditional academic disciplines of geomorphology, soil science, plant science, and animal community ecology. The last approach is preceded with a discussion of the burrowing phenomena as an 'animal-engineering' process.

Since these data bases abstract only recent years and not the early primary literature, this paper represents only a topical overview. The emphasis is on the ecology of semi-fossorial vertebrates, not true fossorial species. Much of the extensive Russian literature was not translated; and the review is biased towards papers written in English. Citations dealing with non-arid environments were occasionally included if relevant. Investigations centering on physiology or genetics are not included. Finally, only a sampling of the available citations involved with each topic below is discussed.

## Results and discussion

### *Natural history*

The principal burrow excavators are the mammals, who often can construct very elaborate, complex burrows with many forks and chambers. Out of 777 genera of terrestrial mammals listed in Walker (1968), 447 are potentially significant in soil disturbance, and 58% of this 447 do so by surface feeding accompanied by burrowing (Paton & Humphreys, 1995). All three orders of reptiles include members that spend time underground by using tunnels built by other animals (Halliday & Adler, 1986) or actively excavating their own. Research describing the natural history of this 'digger/hole' system usually focus on the primary excavator or the resulting burrow.

I categorize primary excavators ('tunnelers') as species in which digging plays the major role in their existence. These are strong and accomplished burrowers who dig a tunnel down into the soil or into a bank. These constructions can be extensive in length and size, are open at the ground surface, and can have major environmental impacts. The epitome of this category would be the armadillo, or antbear (*Orycteropus afer*) in southern Africa, which can excavate burrows spacious enough such that a bovid (the steenbok, *Raphicerus campestris*) can rest in the entrance (Smithers, 1971). The plains vizcacha (*L. maximus*) in Argentina digs very large, complex burrows with many openings (Mares *et al.*, 1989), as does the prairie dog (*C. leucurus*; Sheets *et al.*, 1971) in North America. Primary excavators on a smaller and simpler scale are the Testudinidae of North America, whose distribution (Goin *et al.*, 1962) overlaps much of the distribution of aridisols (Buol *et al.*, 1997); the burrows of these tortoises are comparatively simple but can be deep.

Secondary modifiers are vertebrates that inhabit and modify a burrow dug by a primary excavator. Mammals that are secondary modifiers are often capable of digging their own burrows in soils of lower density but are stopped by a hard pan (e.g.

*Oryctolagus cuniculus* in Australia, Parer *et al.*, 1987; *Ictonyx striatus* in Orange Free State, Lynch 1983). Eastern cottontail rabbits of Florida (*Sylvilagus floridanus*) often are found in inactive gopher tortoise (*Gopherus polyphemus*) burrows in excessively drained thick sands (entisols; Brown *et al.*, 1990) in xeromorphic shrub scrub and sandhill habitats (Myers, 1990), where they frequently modify the opening (pers. obs.). Greer (1989) lists species of Australian Gekkonidae that use the burrows of spiders or lizards, but plug the burrows with dirt. In Arabia the ground gecko *Bunopus tuberculatus* starts burrowing within the burrow systems of desert rodents (Arnold, 1984), and the small pygmy gerbil (*Gerbillus nanus*) frequently begins its digging activities within the warrens of larger rodents (Kingdon, 1990). Snakes can modify burrows by forceful serpentine movements.

A third category would be simple occupants of the burrow who played no role in digging the structure but simply take advantage of its existence. To continue the Florida example, species in this category would be many invertebrates such as silphid beetles (Silphidae), various reptiles (*Anolis carolinensis*), and even birds (*Colinus virginianus*) all of which utilize tortoise burrows (Cox *et al.*, 1987).

Burrow inhabitants frequently found in a certain type of burrow are referred to as commensals. Commensals are further classified into obligate (only found in that particular burrow type) vs. non-obligate categories such as 'occasional', 'frequent', and 'accidental'; the latter three imply that the inhabitant might just as likely use some other type of shelter. While obligates may use another type of shelter for rest or reproduction, it is usually not optimal, since the obligate has a co-evolutionary history with the primary excavator. *Uma exsul*, a desert dwelling lizard, is restricted to areas in which rodents can maintain open burrows year-round (Pough *et al.*, 1978). The distribution of gopher frogs (*Rana capito*) in Florida is restricted to the distribution of gopher tortoises, where the frogs use the burrows as retreats (Godley, 1992). Butts & Lewis (1982) found that 66% of burrowing owls (*Athene cunicularia*) surveyed in Oklahoma, U.S.A., were found in prairie dog burrows, even though the prairie dog towns only occupied 0-16% of the area. They believed that owls nesting in non-prairie dog areas were utilizing marginal habitat (however, see Haug *et al.*, 1993).

Natural history descriptions of burrows frequently classify them according to the apparent function they serve for the user. An early example from the literature is Steiniger (1949, 1950, 1952) for Norway rats (*Rattus norvegicus*): a home burrow used for residence; a food storage burrow located near food sources; and a refuge burrow found near foraging areas. Turner (1972) classified three types of escape burrows used by *Spermophilus beldingi*: short burrows with one entrance, intermediate length burrows with two or three entrances, and long complete burrows. Each are used in response to different alarm calls. Desert tortoises (*G. agassizii*) use two kinds of burrows: winter dens, usually 8-10 feet deep in banks of washes, and summer dens, a shallow hollow dug into the base of an arroyo wall (Ernst & Barbour 1972). Other examples can be found in Shenbrot *et al.* (1997) for *G. dasyurus* (complex burrows with a nest and simple burrows without a nest) and Rogovin *et al.* (1996) for *Pygeretmus pumilio* (day burrows and shelter burrows). These species-specific classifications are useful for explaining species-specific biology but might overlook the possibility that different parts of the same burrow might be used for different reasons (*cf.* Burns *et al.*, 1989 for prairie dogs). Functional ecology of burrowing is discussed below.

The morphological adaptations for burrowing are described in a number of papers. Gekkonid lizards (Diplodactylinae and Gekkoninae) that burrow in the compacted sand of windward dune faces of deserts have webbed feet, used as 'sand shovels' (Bauer & Russell, 1991). Lizards in Arabia have digital fringes which act like snow shoes and which prevent sinking in the sand but also help with digging (Arnold, 1984). An important adaptation in burrowing snakes is the fusion of the brille and postocular; this character was used to re-describe the African colubrid *Elapocalamus gracilis* Boulenger by Resetar & Marx (1981).

The actual burrowing behavior is not as often described. The arid-dwelling bullsnake (*Pituophis melanoleucus*) exhibits head morphology and stereotyped motor patterns adapted to excavating. Spading actions by the snout are followed by scooping a load of sand in a head-neck flexure, moving posterior, and dumping the load away from the excavation at varying distances; an excavating bullsnake can move as much as 3400 cm<sup>3</sup> of sediment per ha (Carpenter, 1982). The desert tortoise (*G. agassizii*) digs by scraping alternately with the forelimbs; when the hole become deep enough the turtle turns around and pushes the dirt out with its shoulders (Ernst & Barbour, 1972).

A number of papers examine attributes of the burrow in semi-arid zones, including below-ground characteristics such as geometry, complexity, and depth (Clark, 1971 for *C. leucurus* in Wyoming; Flosser, 1984 for *Lasiorhinus latifrons* in Australia; Reynolds & Wakkinen, 1987 for *Peromyscus maniculatus*, *Microtus montanus*, *Dipodomys ordii*, and *S. townsendii* in southern Idaho; Hatough-Bouran, 1990 for *Jaculus jaculus* and *G. dasyurus* in Jordan; Bronner, 1992 for several southern African species; Young, 1990 for *S. columbianus* in Alberta; Yensen *et al.*, 1991 for *S. brunnei* in Idaho; Advani & Jain, 1982 for *R. gleadowi* in the Indian desert), soil type (Reynolds & Wakkinen, 1987; Laundre, 1989) and age (Mushinsky & Esman 1994 for *G. polyphemus*). Above-ground habitat variables may play a role in the individual digger's decision to excavate; these include the spatial arrangement of the burrow entrances (Stromberg, 1978 for *C. leucurus* and *C. ludovicianus*), distance to resources such as wet areas (Evans, 1951; Gahr, 1992 for *Brachylagus idahoensis* in Washington) or food patches, cover (Young, 1990 for *S. columbianus* in Alberta; Fitch, 1948 for *S. beecheyi*), and the cryptic nature of the burrow opening (Tognelli *et al.*, 1995 for *Microcavia australis* in Argentina; Kinlaw, 1990 for *Spilogale putorius* in xeric scrub of Florida). In areas where sloped ground is available, some species may seem to prefer it. Zimmerman (1990) reports that *Dasyus novemcinctus* in Oklahoma prefer to burrow in sloped areas. In south-central Florida, armadillos will readily burrow in flat terrain (Kinlaw, pers. obs.) as that is primarily what is available.

### *Functional ecology, burrow architecture, and burrowing behavior*

The historical view of the function of the burrow is that it represents a micro-refuge, or shelter from environmental stresses such as temperature extremes, fire, or predation (e.g. Burns *et al.*, 1989 for *C. leucurus*). Only recently have these claims been substantiated by observational or radio-telemetry studies, modeling, and comparisons of measurements of burrow conditions with those on the surface.

A major problem for vertebrates in desert regions is the high mean diurnal temperature during summer. When the gerbil (*Meriones hurrianae*) of the Thar Desert develops hyperthermia due to continuous exposure to sun, it intermittently visits the cooler environments of the burrow and unloads the excessive heat. This may be the reason that diurnal rodents excavate extensive, multi-tier burrows as compared to the nocturnal rodents (Prakash, 1997). Ground squirrels respond to this environmental stress by using shallower burrows for summer retreats and deeper burrows in winter (Bartholomew & Hudson, 1961). Convincing data that temperatures in deeper parts of burrows are more moderate below the thermal isocline that marks daily fluctuations in soil temperatures have been collected by van Heerden & Dauth (1987) for *Xerus inauris* in southern Africa and Kay & Whitford (1978) for *D. spectabilis* in the Chihuahuan Desert. When thermoregulatory measurements of a burrow dwelling rodent, *Gerbillurus pabea*, and a rock crevice dweller, *Aethomys namaquensis*, were compared, the burrow dweller had a higher rate of conductance to remove metabolic heat produced by the body (Buffenstein, 1984), an adaptation for use of the burrow as a heat sink. Instead of a heat sink, sand goannas (*Varanus gouldii*) in southern Australia use their burrows as a heat trap by re-entering the burrows in the afternoon when burrow temperatures were

still increasing, thus extending the period of elevated body temperature (King, 1980). Desert tortoises (*G. agassizii*) were reported to use burrows as thermoregulatory devices (Woodbury & Hardy, 1948), and they may plug entrances to their burrows to increase this thermoregulatory advantage (Luckenbach, 1982).

A second important obstacle to existence in desert and arid regions is the tremendous dehydration effect of the dry desert air on life-forms. Burrow micro-climate was much more favorable in kangaroo rat burrows than on the surface, since the relative humidity was near saturation (Kay & Whitford, 1978). Similarly, relative humidity in *C. leucurus* burrows was higher than above-ground (Clark, 1971).

Evaporative water loss for desert tortoises (*G. agassizii*) predicted using biophysical models was consistently lower inside burrows than on the surface (Bulova, 1994). Laboratory studies using artificial burrows have generally confirmed these temperature and gas findings.

Seasonal fires represent a common environmental assault, and in plant communities that have co-evolved with fire, burrows play a key role in the population dynamics of both burrowers and non-burrowers. In the Australian heath, five species of *Pseudomys* that burrow commonly survive the acute phase of burns and colonize early successional stages post-fire. After one fire, many carcasses of *Antechinus pseudocheirus*, a non-burrower, were found; the survivors were individuals that took refuge in wombat burrows (Friend, 1993). Pre- and post-fire residency (measured by density, sex ratio, and age classes) of a key burrower in the western U.S. desert, *D. spectabilis*, were unaffected by fire (Levine *et al.*, 1995). Simons (1991) trapped a non-burrower (*Neotoma albigula*) and three burrowers (*D. merriami*, *Perognathus amplus*, and *Chaetodipus baileyi*) before and after a fire in the Arizona Desert. *Neotoma* occupies houses made of sticks and debris that burn intensely, and survival in and emigration from the burned area greatly decreased due to direct mortality. Immediate population changes did not occur in the heteromyids due to the fire, but population sizes did change due to the indirect effect of the lack of vegetational cover in the burned area. The worse environmental extreme imaginable is probably an atomic blast, and kangaroo rats have survived this catastrophe at the Nevada test grounds by remaining in their burrows (Anderson & Allred, 1964).

The morphology and complexity of the burrow can serve an anti-predator function. Potential predators can be thwarted by the diameter, depth, and length of the burrow (Laundre, 1989). Complex, anastomosing burrows can confuse a predator hunting through it for the first time (Bronner, 1992). Some species, such as *Desmodillus auricularis* and *Peromyscus polionotus*, have escape burrows to use as exits, if being pursued. McLean (1978) observed that female Columbian ground squirrel (*S. columbianus*) dug small, inconspicuous chambers on the periphery of the major burrow system which they used for parturition. These small holes were plugged and McLean (1978) speculated that the plugs were responses to predation by non-resident conspecific 'marauding males'. Prairie dogs (*C. ludovicianus*) deposit burrow diggings into a high mound at the burrow entrance, and use the height of the mound to their benefit by perching atop the mound to scan the horizon for predators (King, 1959). The value of burrows and natural cavities in Australia was demonstrated by Smith & Quin (1996) where conilurine rodents have suffered a higher rate of extinction and decline than other mammalian taxa; the investigators attributed this to 'hyper-predation' by cats, foxes, and dingos. Their survey showed a less severe decline in those conilurines which use burrows and natural cavities.

There is an established literature dealing with food hoarding by animals, including desert rodents (see review by Vander Wall, 1990), illustrating that the burrow serves a food storage function. In arid environments, seeds of various Mojave Desert plants will absorb up to 25% of their mass in additional water from vapor in high humidities (Morton & MacMillen, 1982) such as found in a mammal burrow. Kangaroo rats can select seeds that yield more metabolic water (Frank, 1988a) and preformed water

(Frank, 1988 *b, c*). Nagy & Gruchacz (1994) reported that seeds of the creosote bush (*Larrea tridentata*) were a major component of the diet of *D. merriami*, an interesting finding since burrows of this species have been shown to positively influence the growth of creosote (Chew & Whitford, 1992), discussed below.

In species categorized as 'primary excavators', the burrow serves as a focal point for their activities. Radio-telemetered *D. merriami* in the arid Colorado Desert showed a high degree of clustering, which reflected the occupancy of day burrows (Behrends *et al.*, 1985). In the semi-arid scrub of Argentina, radio-telemetered *L. maximus* had a home range centered around a communal burrow system (Branch, 1993).

That the burrow is a key environmental resource can be appreciated when considering philopatry or dispersal. Natal philopatry (retention of offspring in natal home ranges past the age of independence from parents) might be expected to occur more in primary excavators (who have invested much energy in constructing the resource) than non-digging species, especially if the burrower hoards food in the burrow. Jones (1984) demonstrated this phenomena in *D. spectabilis* in south-eastern Arizona. Pfeifer (1980) showed that the limited availability of suitable maternity burrow sites influences juvenile female dispersal in Wyoming ground squirrels (*S. richardsonii*). Secure burrows are critical for mammals with altricial young, which are helpless and vulnerable for many weeks.

It is well known that mole crickets (*Scapteriscus acletus*) and perhaps other burrowing insects use their burrow as an acoustic horn to amplify their calls (Bennet-Clark, 1987). The acoustic properties of the burrow of *Heleioporus*, a burrowing frog from West Australia, were examined by Bailey & Roberts (1981) who found that the burrow enhanced the principal frequency component of the call by resonance. By using suspended microphones, Randall & Lewis (1997) determined that the sealed burrow of foot-drumming kangaroo rats (*D. spectabilis*) provides a quiet place to listen for substrate-borne drummings from conspecifics, and it is known that gerbils can detect low frequency sound such as footfalls on the soil from underground (Kingdon, 1990). Thus, the burrow can serve as a communication device.

From this literature search, I have tabulated nine measured or hypothesized specific functions of burrows. Three of these have survival value: burrows protect from environmental extremes, lessen the risk of predation, and allow access to hoarded food. Burrows are often used as a place to heal from injury or disease; this has obvious survival value, and I have categorized this as a 'hospital' function. Burrows provide a familiar and safe place for reproduction, a population growth function. The downward temperature gradient in deeper burrows provides the opportunity for the occupant to make choices in its position within the burrow, thus allowing more control over its micro-environment (a 'comfort' function). Species that utilize a burrow built by another enjoy a saving of both energy and time since they do not have to invest in the enterprise themselves. Some species not only give birth but rear their young in burrows; thus there is a socialization component to burrow life for these species. Finally, different species have evolved methods to capitalize on the acoustical properties of the burrow chamber for communication.

In a thoughtful essay, Hansell (1993) stresses that burrows and nests have potent biological influences on communities and lists them: (1) the reinforcement of social life; (2) the alteration of habitats; (3) the concentration of resources; (4) the exploitation of the resources of others; and (5) the invasion of new habitats. These influences are usually to the advantage of the burrower.

### *Classical ecological issues*

Three areas of ecology that have a firm conceptual basis are competition theory,

foraging theory, and island biogeography. I now briefly report studies that directly involve the burrow with these three classical issues.

In arid areas a recurring question is 'why are there so many desert rodent species?' Schropfer & Klenner-Fringes (1991) observed that *J. jaculus*, a bipedal rodent, is less attached to its burrow, and uses a wide foraging area in which it finds new food patches frequently. By following this foraging mode, this species only used a small part of the overall resource. They observed that *G. gerbillus*, a quadrupedal rodent, stays close to the burrow, intensively using the area around the burrow, perhaps utilizing close to 100% of the food resource. Their hypothesis is that competition for food is the key, and the extent of this competition is related to the way the burrow is used, in particular the foraging distance from the burrow. Similarly, Bowers & Brown (1992) asked if the proximity of burrows of a dominant species, *D. spectabilis*, affects spatial usage patterns of other rodents in the community? They found that captures of five other species did increase with distance away from *D. spectabilis* mounds. This data is at least congruent with that of Schropfer & Klenner-Fringes (1991) and underscores the importance of the burrow in the community. Regarding competition for space, Layne & Jackson (1994), using radio-telemetry methodology in south Florida, showed that the cotton mouse (*P. gossypinus*) occupies the main tunnel of gopher tortoise burrows, whereas Florida mice *Pedomys floridanus* utilize the inside passages of the same burrow system.

Regarding foraging in arid areas where trees are sparse, ground burrowers hold an advantage over arboreal cavity-requiring species. If the burrow is damaged, they can simply re-excavate near the same food patch. However, if the tree (containing a necessary cavity) is destroyed, the arboreal species will usually need to re-locate to a new position, which would probably be further from a food patch. If the food supply shifts, the burrower can simply follow it, and construct an energy-savings refuge near it. For example, radio-tracked *D. merriami* maintained stable core loci centered around day burrows, but moved to new day burrows once every 4 days (Behrends *et al.*, 1985). A novel rotational use of burrow systems has co-evolved in southern Africa. *Suricata suricata*, *Cynictis penicillata*, and *X. inauris* alternately use each other's burrow system as they move about following shifting food resources (Lynch, 1980). The proximity of a burrow near an extensive food resource also means that the forager can afford to reduce activity during inclement weather conditions. Van Aarde *et al.* (1992) used this hypothesis to explain why radio-tracked armadillo (*O. afer*) reduced foraging activity during cold, dry months in southern Africa.

Vigilance behavior is related to the distance of the forager from the burrow. Holmes (1984) observed foraging hoary marmots (*Marmota caligata*) looking up more with increasing distance from the burrow, and Frase & Armitage (1984) observed yellow-bellied marmots (*M. flaviventris*) foraging closer to the home burrow or refuge burrows than further away. Columbian ground squirrel (*S. columbians*) feed at a quicker rate with increasing distance from their burrow (Andrusiak & Harestad, 1989).

Some North American Heteromyidae occurring in arid regions and that use burrows, frequently cache food in the burrows, as do some Cricetidae in Asia; diagrams and descriptions can be found in Vander Wall (1990). Ellison (1993) dug up burrows of the pouched mouse (*Saccostomus campestris*) at four localities in South Africa and provides a detailed list of the contents of the cache. For the scatter-hoarding *D. merriami*, distance from the burrow was a determinant of where food was initially deposited (Daly *et al.*, 1992).

Since colonization and extinction of micro-communities in these open burrow systems can probably be observed and measured easier than in closed systems (e.g. pocket gopher or mole tunnels), some aspects of island biogeography theory can be tested. Distance from a conspecific's burrow was important in colonizing new sites. Waddell (1986) found, using telemetry, that dispersing *S. columbianus* did not colonize patches of suitable habitat, but rather settled near other squirrels (e.g. burrow systems).

The importance of the burrows for colonization was demonstrated by [Apa \*et al.\* \(1990\)](#), who removed 45% of a *C. ludovicianus* colony by applying rodenticide; the site was re-colonized within 10 months. The importance of site fidelity was further underscored by [Salmon \*et al.\* \(1987\)](#) who completely trapped out a *S. beecheyi* colony and physically destroyed the burrows on a treatment plot, but left intact a control plot. Fifty per cent of the squirrels re-colonized the treatment plot in 5 months (represented 50% of the original population). Interestingly, the burrows were dug in exactly the same location on the treatment plot as they occurred before being destroyed.

Re-colonization is related to prior use. Burrow use patterns may be influenced by chemical cues left by previous inhabitants. Male desert tortoises (*G. agassizii*) were more likely to use burrows treated with another male's chin gland secretion rather than control burrows; females were less likely to use burrows treated with feces from another female than control burrows during the nesting season ([Bulova, 1994](#)).

### *Animals as engineers and resulting impacts*

It is the lack of trees or other vegetative features which could be used as shelter in desert or arid regions that underscore the survival value of underground burrows to the faunal community. In these harsh regions primary excavators are *prima facie* examples of allogenic ecosystem engineers ([Jones \*et al.\*, 1994](#)) that augment the meager shelter options available for vertebrates in arid environments by providing abiotically moderate physical structures. The availability of these energy-saving enclaves across the landscape allow a host of desert species to better optimize their time and energy budgets than if this shelter were not there.

The cumulative effect of these burrow systems depends on the magnitude of six factors (modified from [Jones \*et al.\*, 1994](#)): (1) number of burrows dug in a lifetime; (2) density of burrows in the area; (3) spatial distribution of burrows; (4) length of time species present in the area; (5) durability of the burrow in the absence of original engineer; and (6) number and types of resource flows that are modulated by burrows.

The durability of a burrow may relate to: (1) the type of mechanical motion used to dig; (2) the angle at which it was dug, which is a function of the mechanical digging motion of the excavator; and (3) the substrate. The mechanical mechanism used by many mammals to dig burrows involves digging with a ventro-posterior motion with their paws (from front to rear), and pushing the soil out with their hind feet. The resulting burrows often are simply hollowed out tunnels. Gopher tortoises, on the other hand, dig with a sideways motion, and in doing so compact the soil laterally ([Wilson \*et al.\*, 1991](#)); additionally, the carapace probably exerts some pressure on the roof of the tunnel. The resulting tunnel has a somewhat hardened perimeter; this may play a role in preventing seepage of water into the tunnel, in pulverization of the excavated soil, and in preserving the tunnel over time ([Wilson \*et al.\*, 1991](#)). A Florida investigator has claimed that the tortoise burrow systems can last over 100 years. A second variable affecting the age of the burrow is the angle of repose, the steepest angle at which a substrate will remain cohesive before particles will tumble down due to gravity ([Polis \*et al.\*, 1986](#)). If the tunnel opening drops down at a steep vertical angle, it is more likely to fill up with wind-blown soil, debris, or rain-wash. Some excavators avoid tunnel collapse by digging under roots of trees or shrubs which act to physically support and hold the soil above and around the tunnel. This has been reported in most arid regions (e.g. [Kowalski & Rzebik-Kowalska \(1991\)](#) for *M. libycus* in Algeria; [Smithers \(1971\)](#) for *Tatera leucogaster* in Botswana; [Watts \(1995\)](#) for *P. australis* in Australia; [Gordon \*et al.\* \(1985\)](#) for *Lasiorhinus krefftii* in Australia). The optimal burrow angle in terms of energetic expenditure would be perpendicular to the horizontal ([Polis \*et al.\*, 1986](#)), and desert tortoises will dig directly into the side of a wash ([Luckenbach, 1982](#)), and gopher

tortoises will dig into roadbanks (pers. obs) if these features are available. *Gopherus* is constrained to dig with a sideways swimming motion, resulting in a tunnel that enters the surface at a shallower angle than those dug by mammals which can dig with a downward motion with their forepaws.

When these 'shelter hot spots' have a high spatial density across the landscape, the primary excavator meets the criteria of Power *et al.* (1996) as a keystone species, because the variety of impacts of burrowers in arid ecosystems makes their importance disproportionate to their abundance. After reviewing impacts of burrowing by *G. polyphemus* on xeromorphic shrub occurring on ridges of sandy soil in Florida, Eisenberg (1983) classified this primary excavator as a keystone species. Burrowers in arid regions clearly modify habitats and abiotic factors, and should be referred to as 'keystone modifiers' (Mills *et al.*, 1993). A multi-taxonomic group of vertebrate burrowers that have existed in an area over evolutionary time should be considered a keystone guild because of the cumulative effects of these burrow systems in structuring the faunal community, affecting soil nutrient cycles, impacting plant diversity and succession, and causing major geomorphic changes.

In the sections of this paper that follow, the burrowing phenomena is viewed as an ecosystem process and the impacts of this process are examined from the standpoint of the following traditional disciplines: geomorphology, soil dynamics, plant ecology, animal community ecology, and landscape ecology. An advantage in using this oversimplified and artificial approach is that it allows natural resource scientists an introduction into this ecological phenomena from their own professional orientation.

### *Geomorphology*

Butler (1995) extrapolated from data by various workers on burrows dug in Florida's xeric shrubland soil by gopher tortoises and generalized that this reptile can excavate 40–100 m<sup>3</sup> of sediment per ha. Butler (1995) also extrapolated from data by Kolb (1985, 1991, 1994) on European rabbits (*O. cuniculus*) and derived a figure ranging from 2 to 63 m<sup>3</sup> per ha of sediment displaced. Although Kolb's (1985, 1991, 1994) data were from England, similar magnitudes of soil displacement might apply in arid regions of Australia where they have been introduced. The geomorphic effect may depend on whether the soil had been previously disturbed or loosened. Ground squirrels (*S. townsendii*) and Ord's kangaroo rats (*D. ordii*) both excavated relatively more soil from below 50 cm in disturbed than undisturbed soils (Reynolds & Landre, 1988). Additional data on kangaroo rats (*Dipodomys* sp.) are presented in other papers in this journal volume and will not be reviewed here. Koford (1958) calculated that 12 prairie dog burrows had a volume of 2.7 m<sup>3</sup> and represent the removal of 3.63 metric tons of soil to the surface. However, an additional consideration is the effect of secondary modifiers or predators, especially badgers. Campbell & Clark (1981) reported that 10–27% of the burrows on the sites they studied had been enlarged by badgers in pursuit of prairie dogs.

In the semi-arid regions of Australia, hairy-nosed wombats (*Lasiorninus latifrons*) can burrow through compact soil as well as thick layers of calcrete. The mound created by the tailings can rise 1 m above the surrounding topography (Loffler & Margules, 1980), and large circular areas of bare ground surrounding the burrow opening are created. Although geomorphologic data are not available, Butler (1995) reports that wombats are capable of landform creation and massive sediment displacement. The landscape level effects of wombats are visible from satellite photographs, as are landforms created by viscazcha burrows in arid regions of Argentina (Branch *et al.*, 1996).

After surveying all major phyla of animals that burrow, Butler (1995) recognized that 'although an individual species or genus may not have geographically widespread

geomorphic influence, it may have profound effects locally'; and 'the geomorphic effects of animals must be considered collectively in order truly to be appreciated'.

Hydrology is clearly altered by the burrows. In the cool desert of Idaho, [Laundre \(1993\)](#) compared the amount of water added to the soil profile from spring snowmelt recharge in areas subject to ground squirrel burrowing to that in nearby areas without burrows. He found that recharge amounts in areas with burrows areas were significantly higher than in non-burrow areas. He found that 21% more of the winter precipitation infiltrated into the soil near burrows, and the amount was positively related to burrow density, allowing vertical penetration of the water to deeper portions of the soil profile than in non-burrow areas.

### *Pedological effects*

#### *Effects of burrowing on the soil*

In many environments, burrowing has been shown to affect soil texture and structure, fertility, infiltration, soil mixing, inorganic distribution, mineralization rates, and surface runoff (see reviews by [Reichman & Smith, 1990](#); [Meadows & Meadows, 1991](#); [Butler, 1995](#)). A major burrower in semi-arid regions of North America, the black-tailed prairie dog, has been reported to add organic matter and nutrient salts to the soil, improve the soil structure, and increase water infiltration ([Koford, 1958](#)); enrichment of phosphorus by prairie dogs was reported by [Carlson & White \(1988\)](#). In desert regions, soils are low in nitrogen and phosphorus ([Louw & Seely, 1982](#)), and the concentration of nitrogen-rich feces in and around burrow openings may raise the local nutrient status ([Dean & Milton, 1991](#)).

#### *Effects of the soil on burrow architecture and species distribution*

For vertebrates, burrow structure varies among and within species, and this variation may be related to physical properties of soil ([Anderson & Allred, 1964](#); [Reynolds & Wakkinen, 1987](#); [Reichman & Smith, 1990](#)). The geographic distribution of some burrowing mammals has been related to edaphic factors. Soil structure variables were the main factors affecting distribution of Wagner's gerbil (*G. dasyurus*) in Israel; the preference was for loess mixed with rocks, which permitted easy digging ([Shenbrot et al., 1997](#)). [Weiss & Verts \(1984\)](#) found more pygmy rabbits burrow entrances at sites where soils were significantly deeper and looser than at adjacent sites in Oregon. The complexity or tortuosity of burrows has been shown to be related to the clay and silt content for two rodents, but not a third ([Laundre & Reynolds, 1993](#); [Fig. 1](#)).

[Feldhamer \(1979\)](#) found a direct correlation between density of pocket mice (*P. parvus*) and the percentage of sand, and an inverse relationship with the percentage of clay. In that xeric shrub community, chipmunk (*Eutamias minimus*) density was directly related to percentage of clay in soil, and [Feldhamer \(1979\)](#) suggested that chipmunks did not find it as difficult as the smaller pocket mice to dig through a sometimes hard, consolidated soil surface of high clay fraction. Moreover, a species may alter or eliminate its burrowing activities in unsuitable soils. Hispid cotton rats (*Sigmodon hispidus*) had seven times more burrows systems in Florida on a sandy substrate (Pomello series) than in Kansas on a compact clay humus soil (Oska series) ([Shump, 1976](#)).

### *Vegetation effects*

Burrowing species have been shown to have a variety of effects on arid plant communities. A common finding is that patches are created which promote growth of

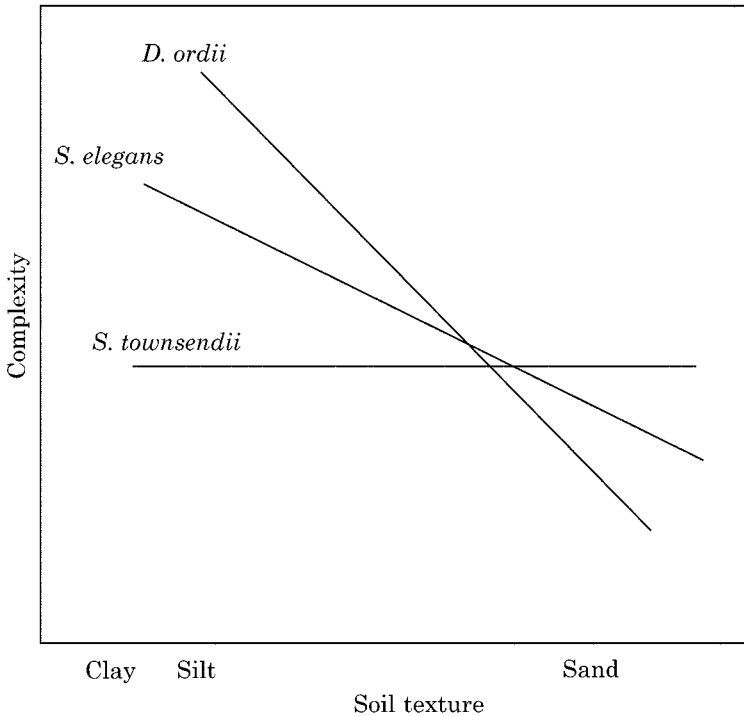


Figure 1. Complexity of burrows dug by three rodents in soils with varying soil textures. Modified from Laundre & Reynolds (1993).

annuals. A burrowing rodent in arid grassy South African dunefields, *T. brandtsii*, maintained circles of bare ground around its warren, creating spaces for annual plants to germinate and grow (Dean & Milton, 1991). Similar findings have been reported for vizcachas (*L. maximus*) in semi-arid scrub in Argentina (Branch *et al.*, in Press), kangaroo rats (*D. spectabilis*) in the Chihuahuan Desert of western U.S. (Moroka *et al.*, 1982; Brown & Heske, 1990; Guo, 1996), and prairie dogs (*Cynomys ludovicianus*) in semi-arid regions of western U.S. (Whicker & Detling, 1988). Arctic ground squirrels, *S. parryii*, were reported to increase the floristic diversity on sand and gravel eskers of non-alpine arctic tundra (Mallory & Heffernan, 1987). A different vegetative composition was found on excavated badger (*Taxidea taxus*) burrow mounds in semi-arid western U.S. (Gibson, 1989), and more pioneer species on gopher tortoise (*G. polyphemus*) mounds on sandhills in Florida (Kaczor & Hartnett, 1990). Since biodiversity is maintained if soil disturbances are small (Futuyma, 1994), the array of small patches created by animal burrows across the landscape should occur at the appropriate scale to stimulate local floristic changes.

#### *Animal community ecology*

Physical structure can interact with ecological processes in varied and complex ways, and influence how communities assemble, function, and persist (contributions in Bell *et al.*, 1991). One of the prime engineering structures that animals build are artifacts that provide shelter for other animals, such as tree cavities, ground burrows, etc. Examples from the literature that report the diversity of species occurring in different sized ground burrows are presented in Table 1. A sampling effect can be seen, as the

Table 1. *Diversity of animal fauna found in burrows in semi-arid environments or environments with dry, sandy soils. Asterick indicates sampling studies; others are observations*

Type of burrow	Diversity	Locality	Reference
Gopher tortoise	302 invertebrates 60 vertebrates	Florida, U.S.A.	Jackson Milstrey, 1989*
Desert tortoise	8 invertebrates, 12 reptiles, 2 birds, 9 mammals	California, U.S.A.	Luckenbach, 1982
Kangaroo rat	14 species of reptiles, 22 families of insects, 6 orders of non-insect arthropods	New Mexico	Hawkins & Nicoletto, 1992*
Aardvark	20 species vertebrates	Southern Africa	Smithers, 1971
Springhare	7 species vertebrates	Southern Africa	Smithers, 1971
Black-tailed prairie dog	82 species invertebrates	Oklahoma	Wilcomb, 1954*

investigations designed specifically to sample the fauna (indicated by asterick in Table 1) have many more species than the casual observations.

Elsewhere in this volume, Ceballos & Pacheco (1997) report increased species richness of small mammals in prairie dog colonies compared to grasslands without prairie dogs. After open burrows are first dug, they often have a sucesional sequence of faunal invasion and colonization. Different species may occupy the burrows for a variety of reasons; the size of the opening appears to be important in burrow selection (Speake, 1981). Taxa that have a co-evolutionary history together may develop patterns of burrow-sharing, ranging from commensalism to obligatory relationships as in the example of *U. exsul* given earlier. Allen & Hoekstra's (1992) view that composition of an animal community is not a happenstance collection but the difference in the organisms because the other community members can be expected to be present, is relevant here. That is, different species might accommodate each other in various ways in the burrow. Thus, burrows dug by these 'keystone' habitat modifiers (Mills *et al.*, 1993) can be critically important for many species and for the ecosystem. In fact, early Russian biologists (e.g. Vlasov, 1937) gave the burrow 'biotope' status. Hawkins & Nicoletto (1992) concluded that the burrows of banner-tailed kangaroo rats can structure the spatial organization of animal communities in the arid grasslands of New Mexico by providing habitat patches that are abiotically moderate and which contain high concentrations of food resources.

In addition to the energetic requirement of constantly maintaining the burrow, there are disadvantages to this mode of existence. Seasonal flooding of burrows has been demonstrated to cause mortality to *T. robusta* (Senzota, 1984) and antedotally linked to decreases in springhare numbers in southern Africa (Lynch, 1983). Invasive species that burrow, such as the imported fire ant (*Solenopsis invicta*), were documented to have a negative relationship with the northern pygmy mouse (*Baiomys taylori*; Killion *et al.*, 1995).

### Summary

Open burrow systems are more than just 'holes in the ground'; they are a major resource for many species. They represent a tractable system for ecological

experimentation. There are fundamental differences in availability and ease of preparation between ground burrows and tree cavities, and this difference may have implications regarding foraging, spacing, and social structure for species that construct each respective resource. There are also differences between 'open' and 'closed' ground burrows, with the former perhaps being more amenable to island biogeographical studies. Questions dealing with the division and use of space by the same or different species within the close confines of the burrow can be addressed. Since the animal is the 'sculptor' and the soil is his medium, incredibly complex designs can be carved out. Faunal diversity may vary with geometry of the burrow. Some species constantly modify their burrow, adding complexity over time; in arid environments where burrow shape can remain intact over long periods of time, I suggest that natural selection will favor this additional spatial resource. What is the relative importance of burrowing as opposed to other types of 'ecosystem engineering' (Jones *et al.*, 1994) in arid zones? Furthermore, there may be principles hidden away in the fields of architectural theory, civil engineering, soil mechanics or soil physics, that may be related to acoustics or longevity of the burrow, when different shapes or designs are compared. Are there major patterns in distribution and abundance of organisms that can be explained by this form of ecosystem engineering? (Jones *et al.*, 1994).

A long-term study in Arizona (Chew & Whitford, 1992) demonstrated an unusual positive impact of mounds of the kangaroo rat on the survival of creosotebush (*L. tridentata*). Similar long-term studies are needed to investigate whether the distribution of plants in arid regions is partly comprised of species which germinated from seeds that were cached in rodent burrows, in view of Naumov & Lobachev's (1975) observation that much of the food of tamarisk gerbils (*M. tamariscinus*) and midday gerbils (*M. meridianus*) store in the wild often is left unused.

This paper has listed some crude similarities in burrowing behavior between endotherms and ectotherms on different continents and the resulting impacts of this burrowing. Are there some central principles of this ecological phenomena between taxa and between habitats, and at different scales? Are there 'assembly rules' of community structure in the micro-communities inhabiting ground burrows, similar to macro-communities (e.g. Diamond, 1975).

Because of the combined effect of open burrow systems on geomorphology, plant communities, and faunal diversity, I suggest that these systems have 'emergent

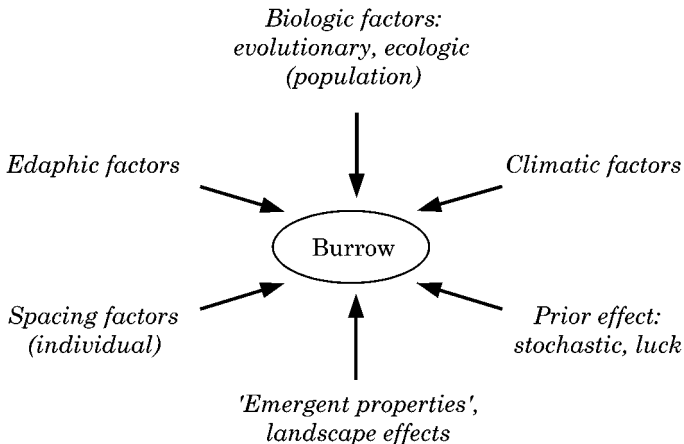


Figure 2. Conceptual model of landscape-level effects of burrow systems. Cellular automata models perhaps could be one approach to model the large-scale patterns that ultimately result from this 'profound local effect'.

properties', that is landscape level effects, illustrated in the conceptual model shown in Fig. 2.

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