

of ecosystem types and should be maintained long enough for species interactions and ecosystem consequences to be observed. The initial stages of altered species composition can be simulated with species addition and removal experiments. However, the long-term changes in community diversity also involve invasion and local extinction, requiring understanding of demographic processes occurring beyond the time scale of most experiments. Demographic and soils par-

ameters should receive particular attention in experimental studies.

(3) Simulation modeling must be an important component of studies that explore the long-term causes and consequences of changes in diversity, particularly those demographic and soils processes that occur too slowly to be examined experimentally. However, these modeling efforts should be closely integrated with field experiments and observations of natural patterns to develop

realistic model scenarios and to provide model predictions that guide further field work.

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Mammalian eusociality: a family affair

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When the term eusociality was first defined¹, it referred to societies of hymenopteran and isopteran insects characterized by a reproductive division of labour, overlapping generations and cooperative care of the offspring of the breeders. Initial attempts to explain the evolution of eusociality were based on genetic and phylogenetic features unique to the social insects^{2,3}. Over the last two decades it has become apparent that eusociality is taxonomically more widespread⁴⁻⁶ and that it lies at the extreme end of a continuum of invertebrate sociality. Many birds and mammals also live in family groups where reproduction is restricted, and these cooperatively breeding vertebrates^{7,8} also meet the criteria for eusociality. However, it was not until close parallels were discovered between the societies of naked mole-rats (*Heterocephalus glaber*) and termites⁹, that a vertebrate was accepted into the eusocial fold and the search for the ecological correlates of vertebrate eusociality began in earnest.

Here we review recent evidence that there are at least two eusocial mole-rats (family Bathyergidae): the naked mole-rat and the Damaraland mole-rat (*Cryptomys damarensis*). The former (Fig. 1a), is a small (\bar{x} =30 g), virtually hairless, poikilothermic¹⁰ rodent from tropical Africa (Fig. 2). Its extensive burrow systems (up to 3.5 km) are dug through soils that are rock hard when dry. The burrows provide the colony, which averages 70–80 mole-rats (maximum at least 295 individuals), with a safe thermostable environment¹¹. The Damaraland mole-rat (Fig. 1b), is a larger (\bar{x} =131 g), haired, endothermic¹² rodent from subtropical

Comparative studies of two species of mole-rat are helping to clarify the ecological correlates of mammalian eusociality.

Both species live in social groups composed of close kin, within which breeding is restricted to one female and one to three males. They inhabit xeric areas with dispersed, patchy food and unpredictable rainfall. During droughts, they can neither expand their tunnel systems nor disperse. In brief periods after rain the animals must cooperate and dig furiously to locate rich food patches. By living in groups, arid-zone mole-rats can take full advantage of windows of opportunity when conditions are right for burrowing. Thus, ecological factors and kin selection have apparently interacted in the evolution of eusociality in these species.

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mole-rats, but different from the three solitary genera of bathyergids (*Bathyergus*, *Georchus*, *Heliophobius*) and from other cooperatively breeding vertebrates, help illuminate some of the extrinsic factors that promoted eusociality.

Two eusocial mole-rats

Naked and Damaraland mole-rats are eusocial according to the classical entomological definition. Each colony typically contains a single reproductive female and one to three reproductive males who breed throughout the year^{13,18,19}. Breeders suppress reproduction in other colony members, mainly through behaviourally mediated stress²⁰.

regions of southern Africa (Fig. 2). It lives in colonies averaging 16 individuals, with a maximum of at least 41. Its burrows, which are dug in softer soils, can be >1 km long; burrow temperatures show considerable seasonal and diurnal variation^{11,13}.

These two species differ physiologically, behaviourally and in the dynamics of colony formation. According to recent mtDNA phylogenies¹⁴, naked mole-rats diverged soon after the bathyergids split from their hystricomorph ancestors, whereas Damaraland mole-rats are of more recent evolutionary origin. If so, the implication is that eusociality evolved twice in the Bathyergidae.

The Damaraland mole-rat provides us with an opportunity to critically re-evaluate some of the characteristics that have been hypothesized as prerequisites for eusociality in the naked mole-rat¹⁵⁻¹⁷. Furthermore, features common to the two eusocial



Fig. 1. (a) The naked mole-rat *Heterocephalus glaber*; (b) the Damaraland mole-rat *Cryptomys damarensis*.

The largest and most-dominant individual in an *H. glaber* colony is the breeding female, while in *C. damarensis* it is the breeding male²¹; the latter is atypical of eusocial societies.

The nonreproductive females of both species are anovulatory and the block to ovarian function appears to be at the hypothalamic level^{22,23}. Spermatogenesis occurs in the nonreproductive males of both species^{13,24}. Significant differences are found in sperm abundance, motility and in the occurrence of abnormalities between reproductive and nonreproductive male naked mole-rats; these differences are not apparent in Damaraland mole-rats²⁵. There is a rapid onset of sexual activity in the nonreproductive females and males of both species when they are experimentally removed from the presence of the dominant reproductives^{13,20,24}.

In both species, nonreproductives are typically the offspring of the breeders or their close relatives (e.g. siblings)^{13,19,26}. Workers forage, maintain and defend their colony in addition to assisting both directly and indirectly in caring for the pups^{8,9,21,26}. Body size is labile and patterns of growth are affected by age and social status. Smaller colony members typically perform more maintenance work than larger ones who usually defend the colony. Workers do not show any morphological specializations (other than size) related to their tasks^{8,18,21,27}. In both species the breeding female is larger than the workers and has a distinctively elongated body^{19,21} that allows her to move freely in the narrow tunnel system during pregnancy. Naked mole-rats produce huge litters (\bar{x} =14 pups, and up to 27 pups) four to five times a year, while Damaraland mole-rats reproduce three to four

times a year and have a mean of three pups, and up to six pups in a litter^{13,19}.

Longevities in captivity can exceed 18 years in *H. glaber* and 10 years in *C. damarensis*. Long-term (>5 years) population studies in the field, however, show that individuals vanish from their natal colonies at a surprisingly rapid rate: <2% of nonreproductive *H. glaber* and <8% of *C. damarensis* were still in their natal colony after three years^{13,26}. Furthermore, <0.1% ($n > 4000$) of *H. glaber* first captured as nonreproductives and 8% ($n > 403$) of nonreproductive *C. damarensis* have been subsequently found as reproductives. This implies that the vast majority of the nonreproductives disappear and probably die before they have an opportunity to reproduce, thus living a lifetime of socially induced infertility.

In contrast, the chance of survival from year to year is far greater for the reproductives, who are usually among the oldest members of the colony^{13,26}. Queen and worker lifespans thus apparently diverge, as in the social insects²⁸. Despite their shorter lifespans, more than one-third of the nonbreeders of both species live at least a year – enough time for them to help rear three or four litters of siblings – and some survive long enough to potentially help rear ten or more litters.

Inbreeding and outbreeding

Important issues with regard to the evolution of cooperative breeding and eusociality are (1) the degree of relatedness of group members, and (2) what promotes colony cohesion. Individuals within a naked mole-rat colony are extremely similar genetically. The average relatedness, based on multilocus DNA fingerprinting, is 0.81, and there is only slightly more variation between neighbouring colonies^{14,29,30}. Such high relatedness is apparently the result of juveniles remaining in their natal colony, new queens being recruited from, and mating within, the colony, and new colonies being founded through fissioning^{18,26}.

Although there are no comparable genetic data on the relatedness of *C. damarensis*, field and laboratory studies reveal strong incest avoidance. New colonies are formed from pairs who originate from different colonies¹³. Colony continuity and integrity is dependent upon the continued presence of the founding reproductive pair¹³. Death or experimental removal of a breeder results in either the cessation of reproduction until a foreign animal is introduced (for as long as five years in captivity), or the splitting up of the colony and the possibility of outbreeding (in the field).

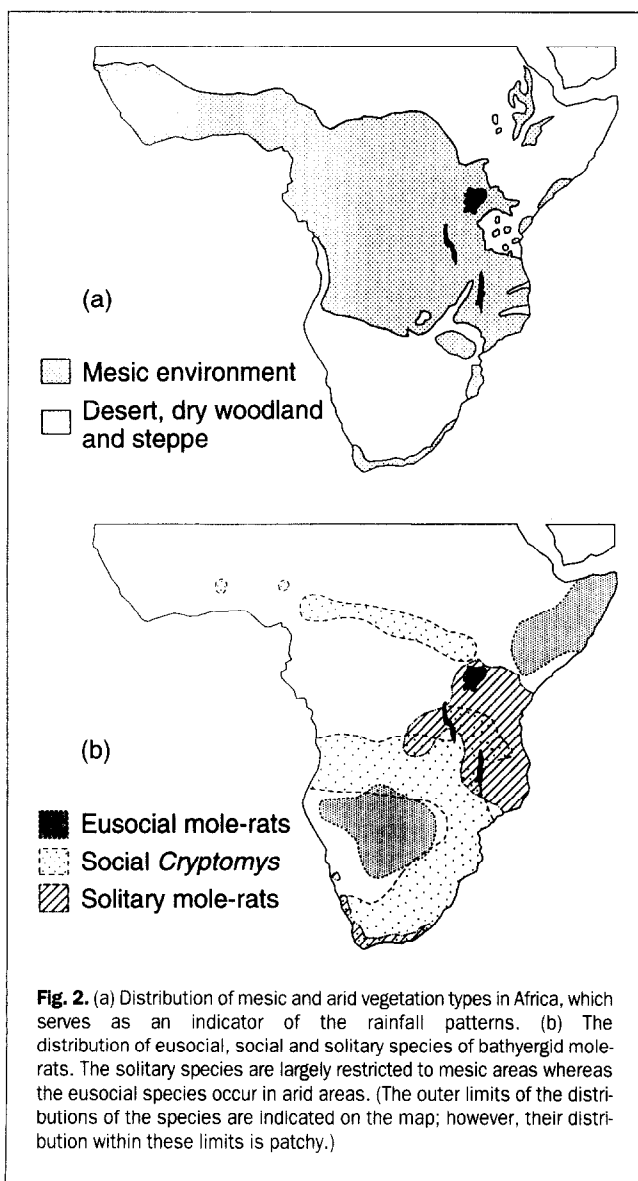
Nonreproductive Damaraland mole-rats thus apparently have a greater chance of breeding than their naked counterparts, but Damaraland mole-rats must leave the colony to do so. Paradoxically, more nonreproductive Damaraland mole-rats are also recaptured over longer periods in their natal colony than are naked mole-rats. Perhaps *C. damarensis* workers are less exposed to predators when making their mounds than are naked mole-rats; the former are protected by the thick core of soil they push out from below, while naked mole-rats kick a fine spray of soil out of an open hole^{13,18}.

Another possibility relates to rainfall. Only one year of average rain has fallen over the five years of our field work (1988–1993) on *C. damarensis*¹³ in Namibia and it is possible that our estimates of philopatry have been inflated by the difficulties the animals have had dispersing. At present, however, recapture data following the one year of average rainfall indicate that nonbreeders in a colony

are not simply awaiting rain for a chance to disperse, but that most will only disperse when a breeder dies. Even then, colonies apparently delay dispersal (sometimes more than a year) until digging conditions are favourable¹³.

Another important difference between the two species is how they treat non-colony members. Naked mole-rats are highly xenophobic and will kill foreign conspecifics that enter their tunnels^{8,26}. Their ability to recognize foreign conspecifics is intriguing because there is so little genetic variability, even in the generally highly variable major histocompatibility complexes, between neighbouring colonies^{29,30}. Damaraland mole-rats are much less aggressive and, in the laboratory, foreign conspecifics can be paired with no apparent aggression.

In most social vertebrates mechanisms exist to prevent or reduce the likelihood of inbreeding³¹. Even the termites, some of which engage in cycles of inbreeding³², embark upon nuptial flights to ensure that outbreeding and dispersal occurs. *Heterocephalus glaber* differs from *C. damarensis* and other social and eusocial animals in having mechanisms that apparently minimize the chance of ever outbreeding. Damaraland mole-rats resemble termites in that they outbreed when environmental conditions are favourable, but differ in that mass dispersal is apparently the result of colonies disbanding after the death of a reproductive.



Dispersal of lone Damaraland mole-rats is occasionally possible, undoubtedly aided by their relatively large body size and endothermy. Nevertheless, the risks are high and only 34 out of 403 marked nonbreeders (8%) that disappeared from their natal colony were subsequently found as breeders. Naked mole-rats are small, poikilothermic and they disperse in groups, which also limits their chances of ever outbreeding^{18,26}. Their xenophobia suggests that different colonies rarely merge.

In naked mole-rat colonies, reproductives are replaced from within, so a new queen may be the sister or aunt of the rest of the colony. Even then, inbreeding ensures that genetic similarity will be high and nonbreeders can still enhance their own inclusive fitness by rearing her pups. Xenophobia helps maintain colony integrity during this transition period, during which fighting for dominance may occur^{8,19}.

In Damaraland mole-rats, all the colony members are the offspring of the reproductive pair. While their parents are alive, most remain in the natal colony and rear siblings. Once a parent dies, however, the risks of dispersal are apparently outweighed by the importance of outbreeding and independent reproduction.

Ecological constraints

All the Bathyergidae are herbivorous and live permanently underground in an elaborate and dynamically changing network of burrows situated within a more permanent home range^{13,33}. Mole-rats feed primarily on subterranean storage organs of plants which they locate as they 'blindly' extend foraging burrows³³. The length of the foraging burrows is related to the biomass of mole-rats occupying the system and to food availability.

In arid areas dry soil may be rock hard (e.g. habitat of *H. glaber*) or the top 25–30 cm may be extremely soft and loose (e.g. habitat of *C. damarensis*). Both soil types are difficult to work. The hard soil rapidly wears down the incisors (digging tools) of the mole-rats. The loose soil cannot be compacted and it pours down into the deeper burrows when the mole-rats dig up to the surface to dispose of the excavated soil. Because of these constraints, both solitary and social species dig most of their foraging burrows when the soil is damp and easily worked, and the energetic cost of burrowing, although still very high³⁴, is at its minimum. Only minor burrow extensions occur outside the rainy season and the excavated soil is then packed into unused tunnels^{13,33}.

The only time when the burrow system is open and the working mole-rats can be taken by predators is as they kick (*H. glaber*) or push (*C. damarensis*) the soil onto the surface. Additionally, the open burrows provide a potential point of entry for predators^{18,26}. Within the narrow confines of the burrows, individuals or small groups of mole-rats are able to defend the colony through heroic acts of aggression toward the predator^{8,18,28,33,35}.

The solitary genera of bathyergid mole-rats inhabit only the more mesic parts of Africa (Fig. 2) where there is a longer and more predictable period during which digging conditions are ideal³⁶, and where severe droughts are rare. Also occurring in these mesic areas are several species of social *Cryptomys*^{17,36,37} (Box 1). Thus, solitary species do not occur in arid regions, but social species are not precluded from mesic areas (Fig. 3).

In the arid regions inhabited by the two eusocial species (Fig. 2), rainfall is unpredictable and prolonged droughts are common. Many plants have underground storage organs (tubers, bulbs and corms), which show

Box 1. Social *Cryptomys*

In addition to the eusocial Damaraland mole-rat, there are at least seven species of *Cryptomys* which live in small colonies^{17,36,38}. In these colonies, a single pair of mole-rats breed, and their non-breeding offspring help dig burrows and care for their younger siblings. Field and laboratory studies on one species, *C. hottentotus*^{36,37}, indicate that cohabitation of individuals in the colony is more transient than in *C. damarensis*. There are, however, no long-term field studies documenting the extent and duration of philopatry of any of these social species of *Cryptomys*.

little seasonal variation in quality or abundance. Many of these geophytes have a dispersed, patchy distribution³³. Once discovered, a single large geophyte or a patch of smaller ones can feed an average-sized colony for a long time³³. The chance of the mole-rats locating such dispersed patches increases when a number of animals join in the search³⁹. When it is dry the soil becomes difficult to excavate, and the costs of burrowing for food, or attempting to disperse, increase dramatically^{13,33}.

During the brief periods when sufficient rain has fallen to moisten the soil, colonies of naked and Damaraland mole-rats can dig more than 1 km of new burrows in a month, depositing several tons of soil on the surface^{13,33}. This activity imposes costly demands on the nonbreeders in a colony, both to locate sufficient food to sustain the colony through dry periods and also to defend it against predators and from incursions of neighbouring conspecifics. Because colonies remain resident in the same home range for many years, the permanent portions of the burrow, the mainline tunnels and deeper nests^{13,18,33}, and the already located food patches, represent valuable, defensible resources which are crucial to the survival of the colony during droughts.

Field studies on Damaraland mole-rats have shown that small, newly founded colonies are the ones most likely to fail, or to be ousted, by larger, stronger neighbouring colonies during a drought¹³. Thus, eight out of 16 small new colonies (2-4 adults) founded following rainfall in January 1991 failed as of January 1993, while only one of eight colonies with an established workforce (>8 adults)

disappeared. Despite the high energy cost of digging in dry soil, and the risk of being the focal point for predators (when no other mole-rats are burrowing), small colonies are the only ones that form mounds during dry seasons. Probably their burrow extensions after rain are not long enough to supply food to sustain them through the drought.

It seems likely that because of these high risks and the severe environmental constraints of frequent and prolonged droughts, the solitary Bathyergidae are unable to live in arid regions.

Why are some mole-rats eusocial?

In the mid-1970s, before the naked mole-rat was known to be eusocial, Alexander²⁸ suggested that if a eusocial mammal did exist it would probably live much like a termite, i.e. in super-safe expandable underground tunnel systems with an ample food supply. This certainly describes the naked mole-rat. The family Bathyergidae, however, contains not one but two eusocial species, as well as three genera that are solitary, and all live in the sort of environment Alexander envisioned. Bathyergids thus provide us with an opportunity to re-examine the factors that have promoted group living and altruistic behaviours. We are particularly interested in what features are exclusive to the eusocial species and common to them (Fig. 3).

Herbivory and living underground in an expansible burrow system separate the eusocial mole-rats from all other cooperatively breeding vertebrates, but are also characteristic of other subterranean rodents (20 genera), most of whom are solitary and xenophobic³⁶.

Despite the relative safety of the underground habitat, both solitary and social bathyergids are vulnerable to predation when they dispose of excavated soil above ground. *Heterocephalus glaber* is particularly vulnerable in this regard because it is the only species in the family to kick soil out of an open hole. We have no evidence of qualitative differences in the types or abundance of predators on solitary versus social species. We do, however, know that Damaraland mole-rats and their solitary congeners are preyed on by cobras and mole-snakes; they also have various other predators in common.

Both solitary and eusocial Bathyergidae live in an environment with similar mean amounts of energy available to them^{33,36}. Over much of the habitat of the two eusocial species food is concentrated into patches of small bulbs and tubers or single larger tubers^{33,39}. In mesic areas the food available to solitary species is generally smaller-sized and more-evenly dispersed³⁶. In the former habitats, the risk of a single animal not finding food are high, and this risk decreases as the number of individuals searching for the food increases³⁹. Thus, it seems that the patchy distribution of food, not its absolute abundance, promotes group living because of the advantage of foraging socially^{39,40}. Huge colonies can sometimes build up on 'islands' of super-abundant food (such as a patch of yams)¹⁸, probably because mortality is lowered (on account of the high-quality food and reduced predation in shorter burrows) and also because there is not enough space within the patch for colony fissioning.

The crucial factor in the evolution of bathyergid eusociality may be the severe restriction of digging imposed by sparse and erratic rainfall and frequent droughts. Unpredictable rainfall has important implications both for finding food and for successfully dispersing. At least 25 mm of rain has to fall within a short period for the soil to become damp enough to work at the depths of the

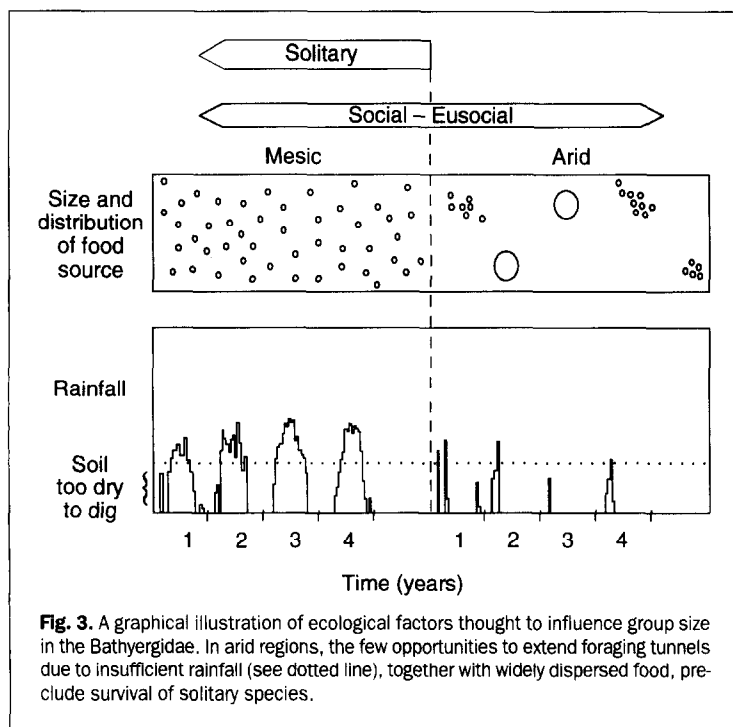


Fig. 3. A graphical illustration of ecological factors thought to influence group size in the Bathyergidae. In arid regions, the few opportunities to extend foraging tunnels due to insufficient rainfall (see dotted line), together with widely dispersed food, preclude survival of solitary species.

mole-rat's foraging burrows (c. 25 cm). In the arid regions of Africa, a single heavy rainfall may provide the only opportunity for a year or more for the mole-rats to locate sufficient food to tide them over until it next rains. In these short periods, a solitary mole-rat would be physically incapable of finding enough food via tunnelling to sustain it over a long drought³⁶. It would also experience considerable difficulty in single-handedly defending a very long burrow. By living in groups, arid-zone mole-rats can take full advantage of windows of opportunity when conditions are right for burrowing. In brief periods after rain, the animals must cooperate and dig furiously to locate food patches.

The unpredictability of rainfall may be one of the reasons why the two eusocial genera breed throughout the year. Continuous breeding would increase the recruitment to the colony and make it more worthwhile for the non-breeders to stay and help if the breeder can constantly supply them with young, needy close kin.

Throughout the evolutionary history of the Bathyergidae, successive prolonged droughts may thus have resulted in 'ecological bottlenecks' which served to exclude the solitary genera from arid regions. Only those species in which the young did not disperse at weaning, but rather remained at home to help, were able to survive in such an unpredictable environment. Some of the seemingly bizarre features of naked mole-rats – for example, lack of hair, poikilothermy, extreme inbreeding and huge colonies – may be red herrings⁴¹ to our understanding of their social evolution. After all, Damaraland mole-rats share none of these attributes but are also eusocial. The unique features of naked mole-rats probably became possible after their highly social lifestyle evolved, and because of the buffered underground niche they occupy.

Only when the Bathyergidae is considered as a whole family is it possible to begin to separate specialized features from those which are fundamental to the evolution of eusociality. Because of the diversity of social groupings shown by this family and the wide range of habitats in which the species occur, research on the family Bathyergidae promises to continue to help illuminate the adaptive significance of vertebrate cooperative breeding.

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