Naked Mole-Rats

Like bees and termites, they cooperate in defense, food gathering and even breeding. How could altruistic behavior evolve in a mammalian species?

Rodney L. Honeycutt

Biological evolution is generally seen as a competition, a contest among individuals struggling to survive and reproduce. At first glance, it appears that natural selection strongly favors those who act in self-interest. But in human society, and among other animal species, there are many kinds of behavior that do not fit the competitive model. Individuals often cooperate, forming associations for their mutual benefit and protection; sometimes they even appear to sacrifice their own opportunities to survive and reproduce for the good of others. In fact, apparent acts of altruism are common in many animal species.

It is easy to admire altruism, charity and philanthropy, but it is hard to understand how self-sacrificing behavior could evolve. The evolutionary process is based on differences in individual fitness—that is, in reproductive success. If each organism strives to increase its own fitness, how could natural selection ever favor selfless devotion to the welfare of others? This question has perplexed evolutionary biologists ever since Charles Darwin put forth the concepts of natural selection and individual fitness. An altruistic act—one that benefits the recipient at the expense of the individual performing the act—represents one of the central paradoxes of the theory of evolution.

In seeking to explain this paradox, biologists have focused their attention on the social insects—ants, bees, wasps and termites. These species exhibit an extreme form of what has been called reproductive altruism, whereby individuals forgo reproduction entirely and actually help other individuals reproduce, forming entire castes of sterile workers. Since reproductive success is the ultimate goal of each player in the game of natural selection, reproductive altruism is a remarkable type of self-sacrifice.

Helping behavior is common in vertebrate societies as well, and some species cooperate in breeding. But until recently there did not appear to be a close vertebrate analogue to the extreme form of altruism observed in social insects. Such a society may now have been found in the arid Horn of Africa, where biologists have been studying underground colonies of a singularly unattractive but highly social rodent.

The naked mole-rat, *Heterocephalus glaber*, appears to be a eusocial, or truly social, mammal. It fits the classical definition of eusociality developed by Charles Michener (1969) and E. O. Wilson (1971), who extensively studied the social insects. In the burrow colonies of naked mole-rats there are overlapping adult generations, and as in insect societies brood care and other duties are performed cooperatively by workers or helpers that are more or less nonreproductive. A naked mole-rat colony is ruled, as is a beehive, by a queen who breeds with a few select males. Furthermore, the other tasks necessary to underground life—food gathering, transporting of nest material, tunnel expansion and cleaning and defense against predators—appear to be divided among nonreproductive individuals based on size, much as labor in insect societies is performed by the sterile worker castes.

The naked mole-rat is not the only vertebrate that can be described as eusocial, but no other vertebrate society mimics the behavior of the eusocial insects so closely. The fact that highly social behavior could evolve in a rodent population suggests that it is time to reexamine some old theories about how eusocial behavior could come into being—theories that were based on the characteristics of certain insects and their societies. In the past decade, since Jennifer U. M. Jarvis first revealed the unusual social structure of a naked mole-rat colony, a number of biologists have been at work considering how a eusocial rodent could evolve. I shall discuss the state of that work briefly here, examining what is known about the naked mole-rat's ecology, behavior and evolution and about altruistic animal societies.

Introducing the Naked Mole-Rat

The naked mole-rat is a member of the family Bathyergidae, the African mole-rats—so named because they resemble rats but live like moles. Many rodents burrow and spend at least part of their life underground; all 12 species of Bathyergidae live exclusively underground, and they share a set of features that reflect their subterranean lifestyle and that demonstrate evolutionary convergence, the independent development of similar characteristics. Like the more familiar garden mole, a mole-rat has a stout, cylindrical body, a robust skull, eyes that are small or absent, reduced external ears, short limbs, powerful incisors and sometimes claws for digging, and a somewhat unusual physiology adapted to the difficulties of life underground, including a burrow

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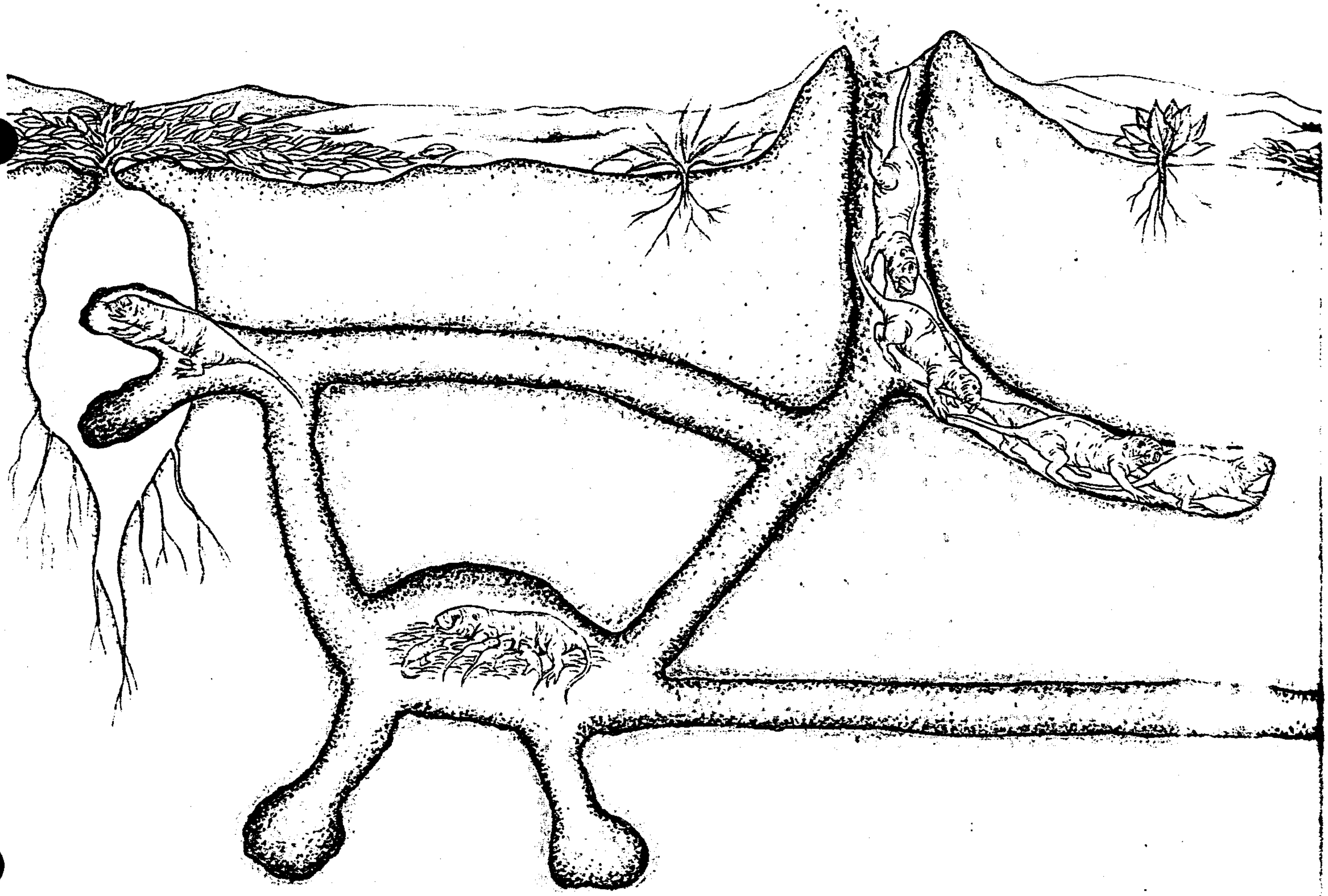


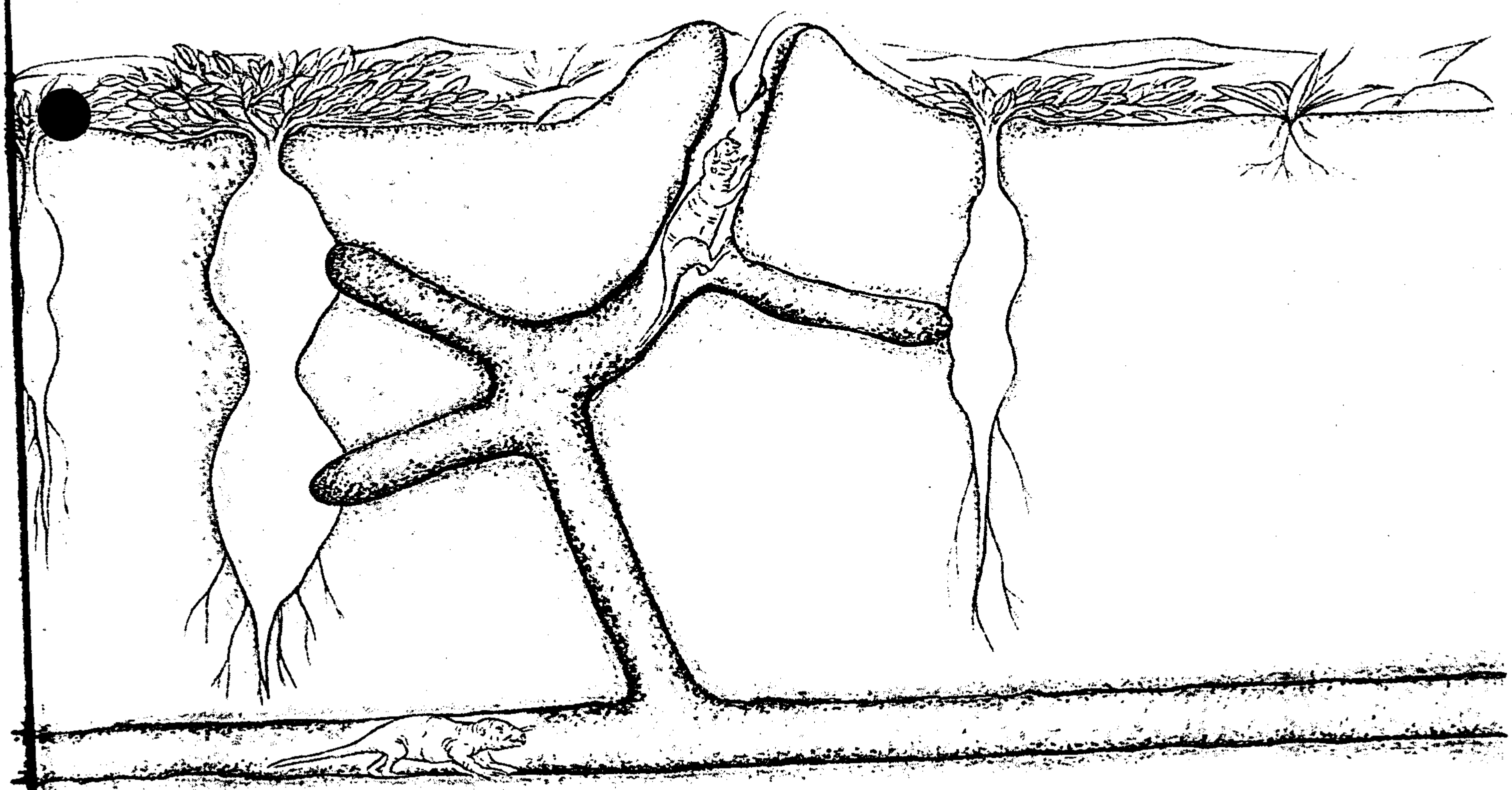
Figure 1. Burrow system built by naked mole-rats beneath the East African desert illustrates the complex social organization that makes the subterranean species unusual. Reproduction in a naked mole-rat colony, which usually has 70 to 80 members, is controlled by a queen, the only breeding female, shown here nursing newborns in a nest chamber. Digging tunnels to forage for food is one of the functions of

atmosphere high in carbon dioxide. All Bathyergidae species are herbivorous, and all but one sport fur coats.

Field biologists who encountered naked mole-rats in the 19th century thought that these small rodents—only three to six inches long at maturity, with weights averaging 20 to 30 grams—were the young of a haired adult. But subsequent expeditions showed that adult members of the species are hairless except for a sparse covering of tactile hairs. Oldfield Thomas, noting wide variations in the morphological characteristics of the naked mole-rats, identified what he thought were several species. *H. glaber* is currently considered a single species, within which there is great variation in adult body size.

Naked mole-rats inhabit the hot, dry regions of Ethiopia, Somalia and Kenya. Like most of the Bathyergidae species, they build elaborate tunnel systems. The tunnels form a sealed, compartmentalized system interconnecting nest sites, toilets, food stores, retreat routes and an elaborate tunnel system allowing underground foraging for tubers *(Figure 1)*. Like the morphology of the animals, the tunnel system is an example of convergent evolution, being similar to those of the other mole-rats in its compartmentalization, atmosphere and more or less constant temperature and humidity. Naked mole-rats subsist primarily on geophytic plants (perennials that overwinter in the form of bulbs or tubers), which are randomly and patchily distributed. The mole-rats forage broadly by expanding their burrows, but their distribution is limited by food supply and soil types. Like most rodents that live underground, they are not able to disperse over long distances.

The tunnel systems of naked mole-rats can be quite large, containing as many as two miles of burrows. The average colony is thought to have 70 to 80 members. In order to study the social organization of the naked mole-rats, biologists have had to devise ways to capture whole colonies and recreate their burrow systems in the laboratory. This is not an easy task, but it is possible because the rodents have a habit of investigating opened sections of their burrow systems and then blocking them. One can create an opening, then capture the naked mole-rats as they come to seal it. Cutting off their retreat requires quick work with a spade, hoe or knife, and the procedure must be repeated in various parts of the tunnel system in order to retrieve an entire colony. A carefully reconstructed colony can survive quite well in captivity, and naked mole-rats are beginning to become an attraction at zoos.



nonreproductive workers, which often form digging teams; one individual digs with its incisors while others kick the dirt backward to a mole-rat that kicks it out of the tunnel. The molehills or "volcanoes" formed in this way are plugged to create a closed environment and deter predators such as the rufous-beaked snake. Tubers and bulbs are the naked mole-rats' food source.

Most African mole-rats excavate by digging with their large incisors, removing the dirt from the burrow with their hind feet. The digging behavior of naked mole-rats, which are most active during periods when the soil in their arid habitat is moist, appears to be unlike that of the other mole-rats in two respects. First, instead of plugging the surface opening to a tunnel during excavation, the naked mole-rats "volcano," kicking soil through an open hole to form a tiny volcano-shaped mound. When excavation is complete, the tunnel is plugged to form a relatively airtight, watertight and predator-proof seal *(Figure 4)*. Second, naked mole-rats have been observed digging cooperatively in a wonderfully efficient arrangement that resembles a bucket brigade. One animal digs while a chain of animals behind move the dirt backward to an

Figure 2. Wrinkled, squinty-eyed and nearly hairless, the first naked mole-rats found by biologists were thought to be the young of a haired adult. The rodents are just three to six inches long at maturity, although there is great variation in body size within each colony. Other morphological features reflect the fact that the naked mole-rats live entirely underground: small eyes, two pairs of large incisors for digging, and reduced external ears. (Except where noted, photographs courtesy of the author.)

Figure 3. Habitat of the naked mole-rats is hot, dry and dotted with patches of vegetation. Visible in the foreground of this photograph, taken in Kenya, are the molehills formed by the rodents.

Figure 4. "Volcanoes" formed when naked mole-rats kick sand out of a tunnel, then plug the opening, make the animals' burrows easy to find. Naked mole-rats are most vulnerable to predators while forming volcanoes; the activity often attracts the attention of snakes.

animal at the end, which kicks the dirt from the burrow. One 87-member colony was seen to remove about 500 kilograms of soil per month by this process. Another colony of similar size moved an estimated 13.5 kilograms in an hour—about 380 times the mean body weight of a naked mole-rat. A team kicking dirt through a surface opening is vulnerable to attack from snakes; the mounds also make *H. glaber*'s colonies easy for scientists to find.

Naked mole-rats are long-lived animals and prolific breeders. Several individuals caught in the wild are surviving after 16 years in captivity; two of these are females that still breed. In captive colonies females have produced litters as large as 27, and in wild populations litter sizes can be as high as 12. The naked mole-rat breeds year-round, giving birth about every 70 to 80 days. This fecundity is unusual among the Bathyergidae. The other highly social species of African mole-rat, *Cryptomys damarensis*, is also a year-round breeder but produces smaller litters, with an average size of five.

The major threat to the longevity of a naked mole-rat, and probably to all of the mole-rats, is predation. On at least two occasions I have encountered the rufous-beaked snake in a mole-rat burrow; one snake had three mole-rats in its stomach. Similar field observations have been made by other investigators. Encounters between mole-rats and snakes in the laboratory suggest that avoidance may not be the mole-rat's only strategy against predators; individuals have also been seen attacking the predator in their defense of the colony.

The naked mole-rat's closest relatives are the 11 other species in the Bathyergidae, which are all of exclusively African origin and distribution *(Figure 5)*. It has been difficult to determine which of the 32 other rodent families shares a common ancestry with the Bathyergidae, but a consensus arising from recent studies places the family in the rodent suborder Hystricognathi, which includes caviomorph rodents from the New World—porcupines, guinea pigs and chinchillas—and porcupines and cane rats from the Old World. The naked mole-rat is the most divergent species within the Bathyergidae, its evolutionary branch splitting off at the base of the family's phylogenetic tree *(Figure 6)*.

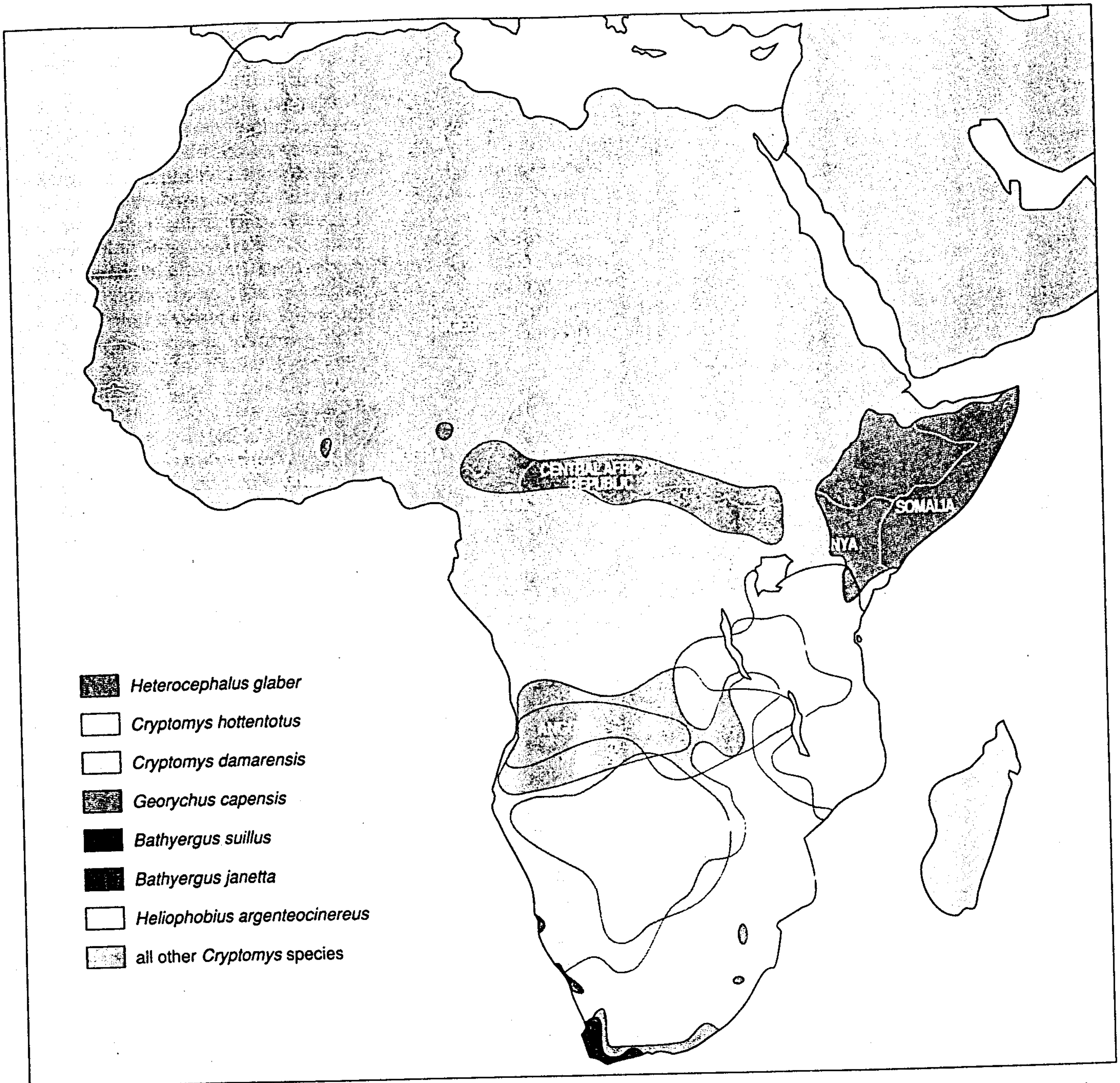


Figure 5. Geographic range of the naked mole-rat, *Heterocephalus glaber*, is limited to the hot, dry region called the Horn of Africa—parts of Ethiopia, Kenya and Somalia. On the map are shown the areas inhabited by other species of African mole-rats. All species in the family Bathyergidae live entirely underground. Most are solitary or colonial; the other species with a highly developed social structure, *Cryptomys damarensis*, is found in Southern Africa.

How Do Altruistic Societies Evolve?

Darwin called the development of sterile castes in insect societies a "special difficulty" that initially threatened to be fatal to his theory of natural selection. His solution to the problem was surprisingly close to current hypotheses based on genetic relatedness, even though he did not have a knowledge of genetics. Darwin suggested that traits, such as helping, that were observed in sterile form could survive if individuals that expressed the traits contributed to the reproductive success of those individuals that had the trait but did not express it.

Today the notion of *inclusive fitness* forms the foundation for theories about how reproductive altruism might evolve. The idea arose in 1964 from William Hamilton's remarkable genetic studies of the Hymenoptera, the insect order that includes the social ants, bees and wasps. Hamilton showed that if the genetic ties within a generation are closer than the ties between generations, each member of the generation might be motivated to invest in a parent's reproductive success rather than his or her own. Inclusive fitness is a combination of one's own reproductive success and that of close relatives.

In the Hymenoptera, Hamilton found an asymmetric genetic system that could contribute to the development of reproductive altruism by giving individuals chances to maximize their inclusive fitness without reproducing. Hymenopteran males arise from unfertilized eggs and thus have only one set of chromosomes (from the mother); females have one set from each parent. The males are called haploid, the females diploid, and this system of sex determination is referred to as *haplodiploidy (Figure 9)*. The daughters of a monogamous mother share identical genes from their father and half their mother's genes; they thus have three-quarters of their genes in common. A female who is more closely related to her sister than to her mother or her offspring can propagate her own genes most effectively by helping create more sisters. Sterile workers in hymenopteran insect colonies are all female.

Hamilton's work prompted a flurry of interest in genetic asymmetry, but he and others recognized that it was not a general explanation for how eusocial societies might evolve. There are many limitations; for instance, multiple matings by females reduce the closeness of relationships between sisters, and it is hard to explain the incentives for females to tend juvenile males, which are not as closely related as are sisters. Furthermore, although eusociality has evolved more times in the Hymenoptera than in any other order, it has also evolved in parts of the animal world in which both sexes are diploid— namely Isoptera, which includes the social termites, and Rodentia, the order that includes the naked mole-rat. Finally, there are many arthropod species that are haplodiploid and have not developed highly social behavior.

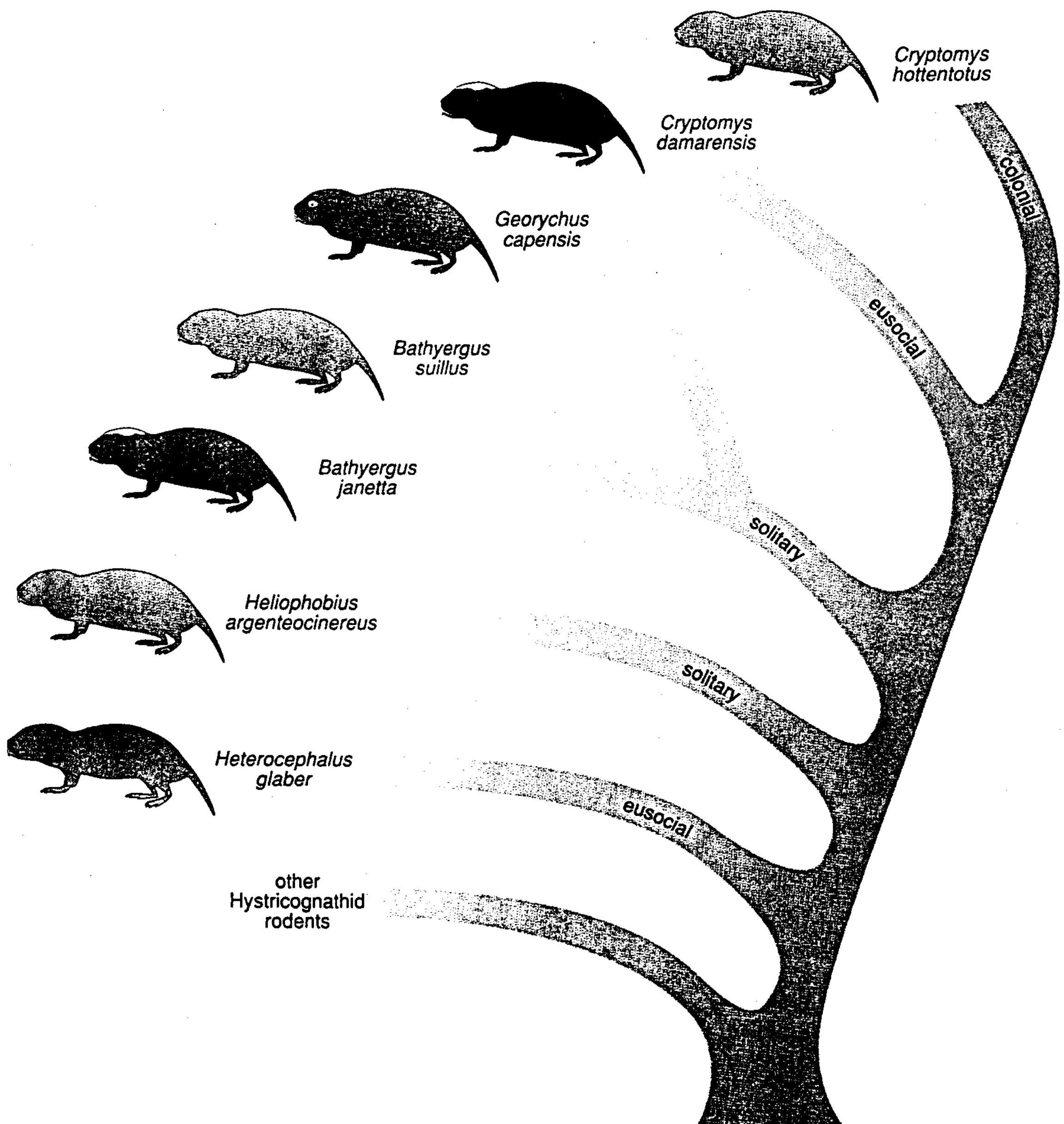


Figure 6. Phylogenetic tree for the family Bathyergidae, the African mole-rats, shows that the two eusocial, or truly social, species are quite divergent. Among other rodents, the suborder Hystricognathi, which includes porcupines, guinea pigs and chinchillas, appears to have the closest genetic link with the African mole-rats. Although there is much similarity among the Bathyergidae species in their physiological characteristics and their subterranean lifestyle, the phylogenetic distance between the eusocial species of mole-rats suggests that complex social behavior evolved separately in the two cases.

There is another way that close kinship might develop among the members of a generation, and it is considered a possible explanation for the evolution of the termite and naked mole-rat societies. Several generations of inbreeding could result in a higher degree of relatedness among siblings than between parents and offspring *(Figure 10)*. When male and female mates are unrelated, but each is the product of intense inbreeding, their offspring can be genetically identical and might be expected to stay and assist their parents for the same reasons set forth in the haplodiploid model. The inbreeding model was developed by Stephen Bartz in 1979 to explain the development of eusocial behavior in termites, which live in a contained and protected nest site conducive to multigenerational breeding.

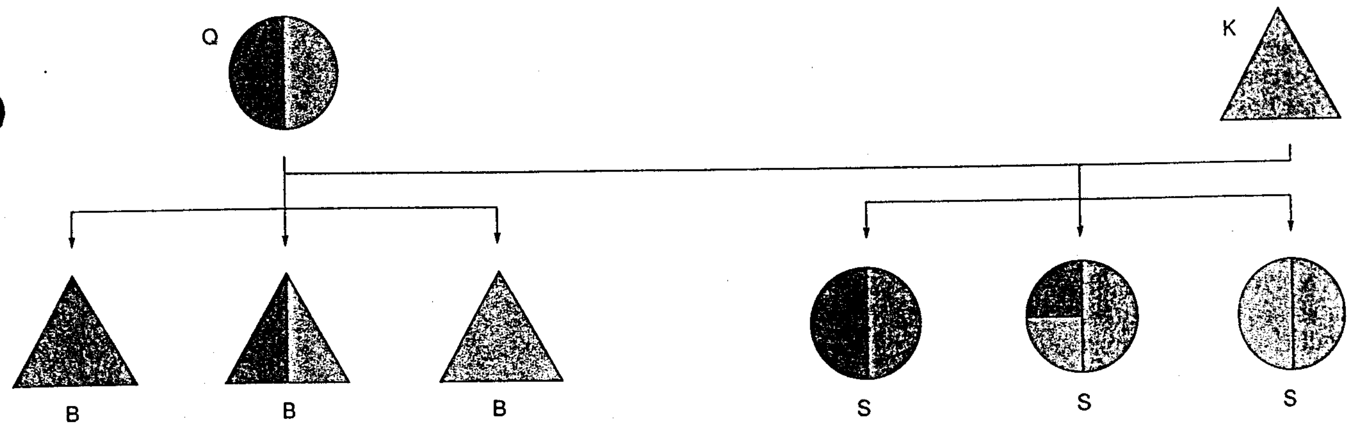
Genetics alone cannot provide a comprehensive explanation for the evolution of eusociality. Other possible explanations, especially relevant to termites and vertebrate helpers, lie in combinations of ecological and behavioral factors. These factors perhaps provided preconditions or starting points for the eventual evolution of a eusocial lineage or species. The best way to understand the development of eusociality may be to consider the costs and benefits associated with remaining in the natal group and helping, as compared to the costs and benefits of dispersing and breeding.

Probably one of the most important preconditions for the development of eusociality is parental care in a protected nest, where offspring are defended against predators and provided with food. If there is a high cost associated with dispersal—in terms of restricted access to food, lack of breeding success or increased vulnerability to predators—then there may be an incentive for juveniles to remain in the protected nest and become helpers. Helpers that remain in the nest for multiple generations may forgo reproduction indefinitely as a consequence of maternal manipulation.

The short-term benefits of group living seem to accrue mainly to those individuals who are reproducing, since they benefit from the help others provide with defense and obtaining food. In fact, there is a correlation between the breeder's reproductive fitness and the number of helpers in cooperatively breeding vertebrate species. Thus the long-term effect of helping may be an

Figure 7. Catching naked mole-rats requires some understanding of their behavior. Mole-rat catchers create an opening from the surface to a burrow, which is normally kept sealed by the animals, and wait quietly for a mole-rat to investigate. A spade, hoe, pick or knife blade is driven quickly into the tunnel to block the mole-rat's escape. (Photograph courtesy of Stan Braude, University of Missouri at St. Louis.)

Figure 8. Captive naked mole-rats, carrying identifying tattoos, adapt well to being placed together in bins, apparently because the highly social animals tend to huddle together for warmth in their burrows in the wild. These rodents are part of Jennifer U. M. Jarvis's collection at the University of Cape Town.



degrees of relatedness in haplodiploid species

	daughter	son	mother	father	sister	brother
female	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{3}{4}$	$\frac{1}{4}$
male	1	0	1	0	$\frac{1}{2}$	$\frac{1}{2}$

Figure 9. Haplodiploidy, an asymmetric genetic system, is thought to contribute to the development of reproductive altruism in ants, bees and wasps—species with intricate social systems that include sterile castes of workers. In a haplodiploid species, males *(triangles)* arise from unfertilized eggs and have only one set of chromosomes, whereas females *(circles)* have one set of chromosomes from each parent. The relatedness between sisters—the fraction of their genes that are shared—is thus greater than the relatedness of mother and daughter *(bottom panel)*. William D. Hamilton hypothesized that females seeking to increase their inclusive fitness—a combination of their own reproductive success and that of close relatives—might in a haplodiploid species become helpers, advancing the continuation of their own genetic heritage by helping with the reproduction of sisters rather than their own offspring. Although haplodiploidy is not considered a full explanation of how eusocial behavior would evolve in ants, bees and wasps, it is notable that most species in which reproductive altruism has evolved are haplodiploid, and that the sterile workers among the haplodiploid insects are all female. In this illustration, the parents are labeled *Q* and *K* and the offspring *S* and *B*, following the scheme in Figure 10; for simplicity, the effects of any recombination of genes are not depicted.

increase in inclusive fitness for the helpers. This may prove to be a very important consideration in species where the probability of a dispersing individual procuring a nest site and eventually breeding is extremely low.

Naked Mole-Rat Society

In some ways the social organization observed in naked mole-rat colonies is more akin to the societies of the social insects than to the social organization of any other vertebrate species. In other respects, mole-rats are unique and may always remain a bit of a mystery.

Some similarities between naked mole-rat societies and the insect societies are striking. A naked mole-rat colony, like a beehive, wasp's nest or termite mound, is ruled by its queen or reproducing female. Other adult female mole-rats neither ovulate nor breed. The queen is the largest member of the colony, and she maintains her breeding status through a mixture of behavioral and, presumably, chemical control. She is aggressive and domineering; queenly behavior in a naked mole-rat includes facing a subordinate and shoving it along a burrow for a distance. Queens have been long-lived in captivity, and when they die or are removed from a colony one sees violent fighting among the larger remaining females, leading to a takeover by a new queen.

Most adult males produce sperm, but only one to three of the larger males in a colony breed with the queen, who initiates courtship. There is little aggression between breeding males, even upon removal of the queen. The queen and breeding males do not participate in the defense or maintenance of the colony; instead, they concern themselves with the handling, grooming and care of newborns.

Eusocial insect societies have a rigid caste system, defined on the basis of distinctions in behavior, morphology and physiology. Mole-rat societies, on the other hand, demonstrate behavioral asymmetries related primarily to reproductive status (reproduction being limited to the queen and a few males), body size and perhaps age. Smaller nonbreeding members, both male and female, seem to participate more in gathering food, transporting nest material and clearing tunnels. Larger nonbreeders are more active in defending the colony and perhaps in removing dirt from the tunnels. Jarvis has suggested that differences in growth rates may influence the length of time that an individual performs a task, regardless of its age.

Naked mole-rats, being diploid in both sexes, do not have an asymmetric genetic system such as haplodiploidy. As Bartz has proposed for termites, inbreeding in naked mole-rats may create a genetic asymmetry that mimics the result of haplodiploidy. There is genetic evidence suggesting that naked mole-rats are highly inbred within colonies and even between colonies in a local area. An important part of the question about breeding within and between colonial groups cannot be answered, however, since there is very little information on how mole-rat colonies are established. This makes it difficult to evaluate the naked mole-rats using Bartz's model of inbreeding and eusociality in termites.

Still, among the eusocial insects termites offer the closest comparison with the naked mole-rats. Termites are the only eusocial insects outside the Hymenoptera, and all termites are diploid, with two sets of chromosomes. Worker groups include nonreproductive males and females, and they perform primarily tasks associated with maintaining and defending the colony. The queen termite is more passive than a naked mole-rat queen and uses chemical control. Termite colonies are much larger, sometimes having more than 10,000 workers, and the definition of castes is more rigid.

The naked mole-rat cannot be considered the only eusocial vertebrate species, but it does represent the most advanced form of vertebrate eusociality and the one most analogous to eusociality in insects. Helping or cooperative breeding has evolved many times in vertebrates, and in many of those species the social system includes both a small number of reproducing individuals (usually a dominant breeding pair) and several nonbreeding individuals (males and females), representing offspring from previous years, that serve as helpers or alloparents. As in naked mole-rats, these nonbreeders participate in foraging for food, care of young and defense against predators. Unlike naked mole-rats, most cooperatively breeding vertebrates (an exception being the wild dog, *Lycaon pictus*) are dominated by a pair of breeders rather than by a single breeding female. The division of labor within a social group is not as pronounced in other vertebrates, and the colony size is much smaller. In addition, mating by subordinate females in many social vertebrates is not totally suppressed, whereas in naked mole-rat colonies subordinates are not sexually active, and many may never breed.

Several ecological and behavior factors may have facilitated the evolution of eusociality in naked mole-rats. Richard Alexander, Katharine Noonan and Bernard Crespi (1991) have sug-

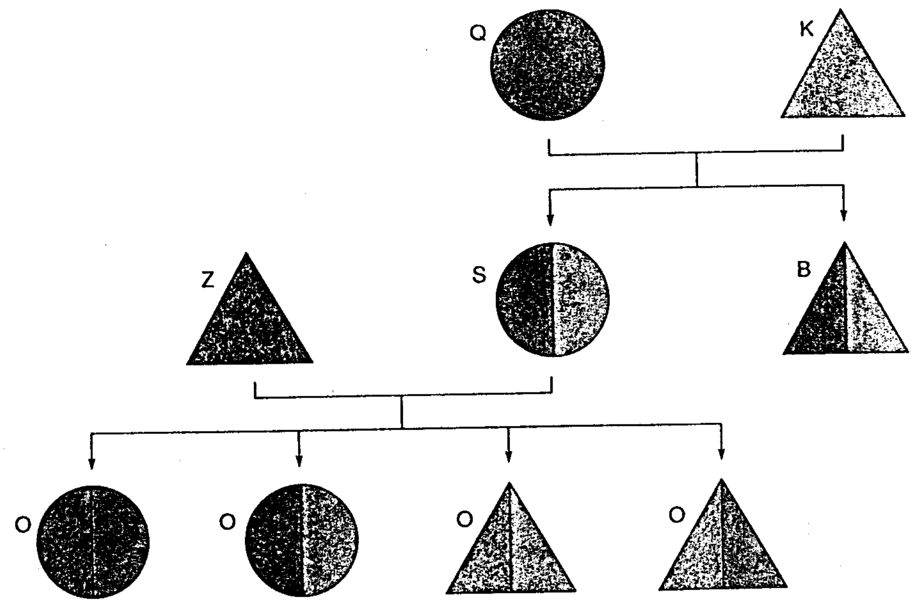


Figure 10. Genetic asymmetry can be produced by cycles of inbreeding and outbreeding in a way that may encourage the evolution of reproductive altruism. Stephen Bartz developed a genetic model to explain how complex social behavior could have evolved in termites living within the confines of a bark-covered chunk of rotting wood. Bartz's hypothesis begins with the mating of a male and a female who are unrelated but are each the product of intense inbreeding (the "queen" and "king," or *Q* and *K*, *above*), so that for each, both halves of the genotype are essentially identical. The products of this union (*S* and *B*) are essentially identical and therefore more related to one another than to their parents; this genetic asymmetry is thought to encourage helping behavior in both sexes because each sibling can increase its inclusive fitness by assisting in the creation of brothers and sisters. If one of the offspring mates with a similarly inbred but unrelated individual, as in the case of *S* and *Z*, the new parents and the new offspring (*O*) are less closely related than than are the original siblings, *S* and *B*. The result mimics the close ties between siblings that are produced by haplodiploidy (*Figure 9*), but the genetic asymmetry disappears in subsequent generations unless specific patterns of inbreeding and outbreeding are followed. (Adapted from Bartz 1979.)

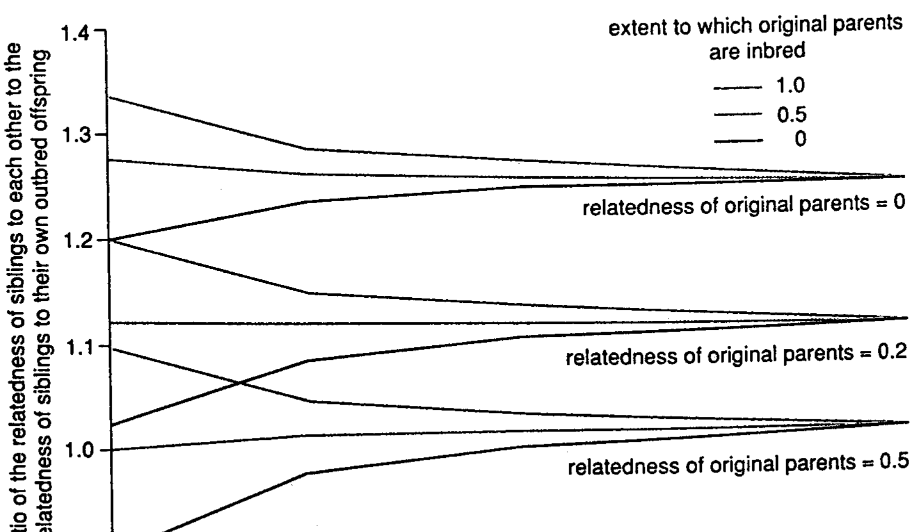


Figure 11. Brother-sister incest might perpetuate the genetic asymmetry shown in Figure 9 over several generations. On this graph, a ratio of relatedness greater than 1.0 means that siblings are more related to one another than to their offspring and are therefore encouraged to become helpers rather than breeders. It is evident that helping behavior is most encouraged when the original parents are highly inbred but unrelated; brother-sister mating makes the inbreeding of the parents unimportant after a few generations, but the importance of the relatedness of the original parents persists. A similar pattern might have contributed to the evolution of social behavior in the confined quarters in which naked mole-rats breed. (From Bartz 1979.)

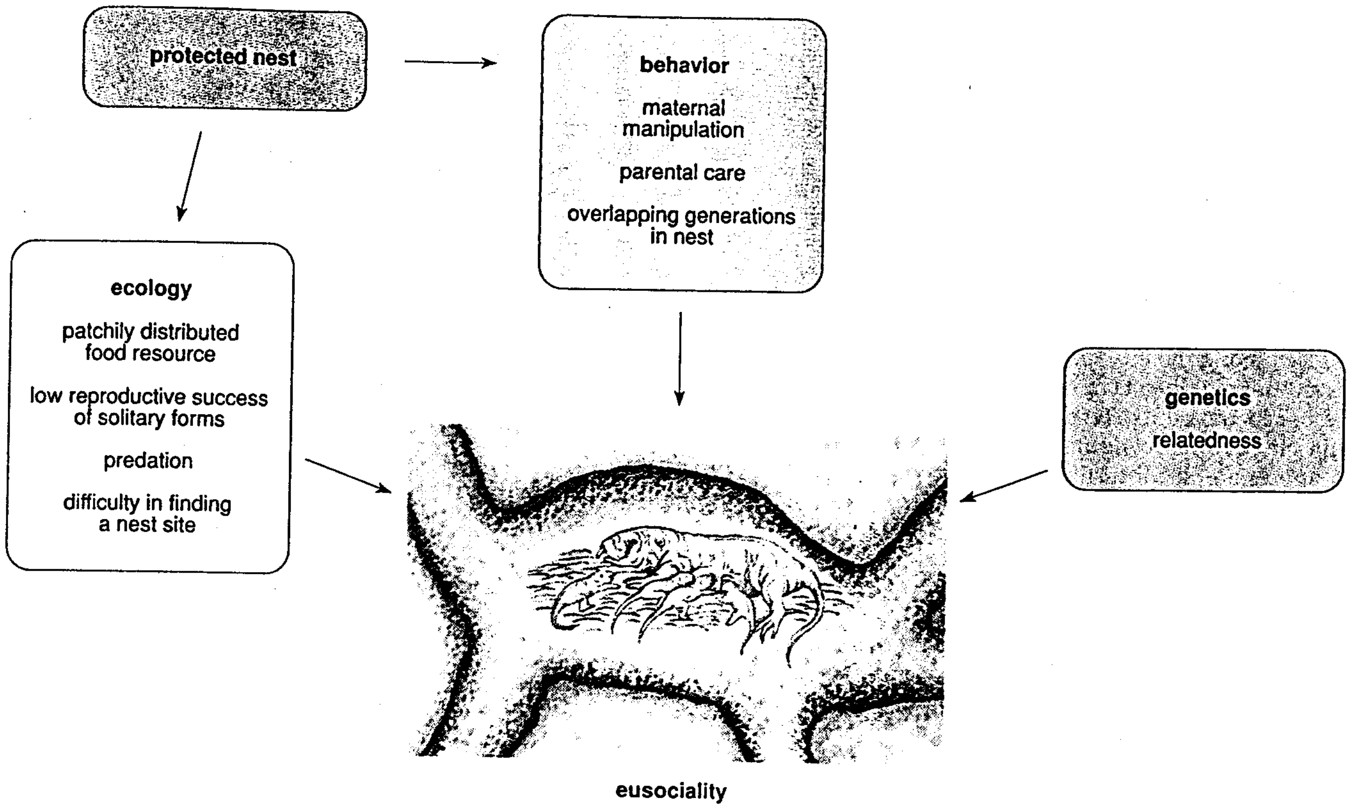


Figure 12. Genetic, ecological and behavioral factors probably combine to promote the development of eusociality in an animal species. All of the factors shown above may have been important in the evolution of the complex social organization of naked mole-rat colonies. Inbreeding in the rodents' underground burrows may have created a high degree of genetic inbreeding within generations, promoting helping behavior. In the ecosystem inhabited by the naked mole-rats, the costs associated with leaving the nest may be high compared to the benefits of group living. Behavioral patterns such as parental care may also have predisposed the species to large-scale group living. A closed burrow system that provides a protected nest environment might be crucial in tipping the ecological and behavioral balance toward organized group living and cooperative breeding.

Figure 13. Ruler of a famous group of naked mole-rats, the queen of Jennifer U. M. Jarvis's captive colony at the University of Cape Town in South Africa is distinguished from her subjects by her large size. She is still breeding after 16 years of captivity. Jarvis's colony served as the basis for the first description of eusocial behavior in a mammal.

gested that the subterranean niche shared by termites and naked mole-rats may be an important precursor for the evolution of eusociality. Life underground provides relative safety from predators and access to a readily available food source that does not require exit from the underground chamber. It also offers an expandable living place that can accommodate a large group.

Since the naked mole-rats share their subterranean niche with the other mole-rat species, it is interesting to speculate about why eusocial behavior has or has not evolved among the other Bathyergidae. Of the other 11 species, all are solitary but two—one of which, *Cryptomys damarensis*, may be termed eusocial. *C. damarensis* is not a particularly close relative of the naked mole-rat; whereas *H. glaber* diverged at the base of the family phylogenetic tree, *C. damarensis* is a distantly related and much more recent species, suggesting that complex social behavior in the two species evolved quite separately *(Figure 6)*. Another species in the *Cryptomys* genus, *C. hottentotus*, is the only other social member of the family; its small colonies (two to 14 members) have less well-developed social structures and vary in size and organization.

C. damarensis colonies are somewhat smaller than those of the naked mole-rat, having eight to 25 members. They also include a single reproductive female and one or more reproductive males and exhibit a division of labor among reproductive individuals based on size. One important difference between the two species has been suggested: *C. damarensis* colonies appear to be less stable over time, and the effects of multigenerational group living and inbreeding may be less pronounced. The significance of the presumed differences is a matter that will require further study because the dynamics associated with the duration of colonies and the founding of new colonies in wild naked mole-rats are not well understood. For instance, new colonies presumably are formed from existing colonies by budding, or fissioning, but the frequency of this event and its causes are not known.

The features of the subterranean niche may supply part of the explanation of social living in mole-rats, even though many solitary, non-social species of rodents in the Bathyergidae and other families occupy a similar niche. Restricted access to food and an unpredictable environment may also provide clues to the evolution of eusociality in both naked mole-rats and *C. damarensis* because as resources become more difficult to find, the energetic cost associated with finding them increases. Several authors have suggested that cooperation in food foraging and communal living might be promoted by the patchy distribution of the food source.

There is no simple explanation for the evolution of eusociality, and the hypotheses that fit the naked mole-rats and the other social species should not be considered mutually exclusive. Reproductive altruism is more likely to occur among genetically related individuals, but relatedness is not a sufficient explanation. Each eusocial species has a unique combination of life-history characteristics associated with both its ecology and its behavior, and some or perhaps all of these characteristics may have predisposed a particular species for group living and cooperative breeding. The fact that various factors can work together in the development of eusociality may provide the ultimate explanation for the novelty, and therefore the mystery, of each example of eusocial behavior.

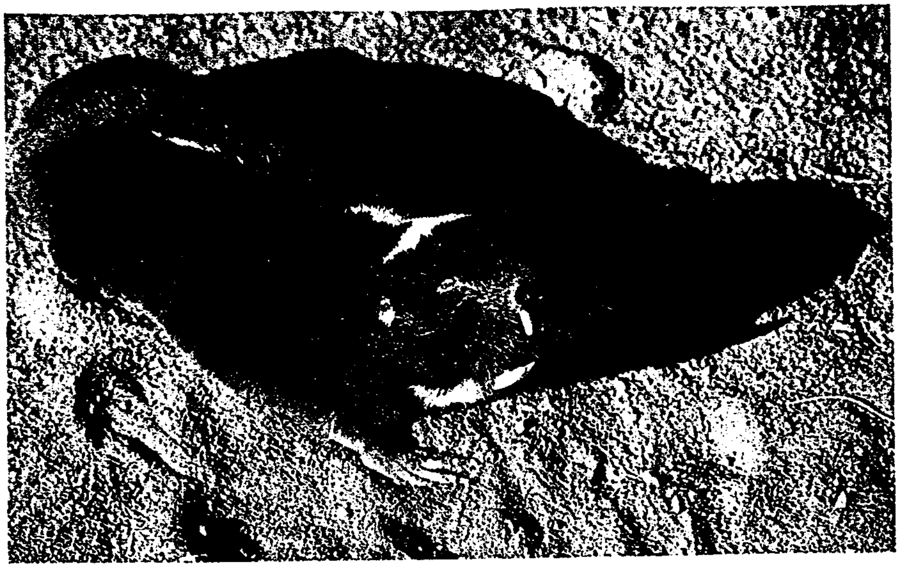


Figure 14. *Cryptomys damarensis* is an African mole-rat distantly related to the naked mole-rats but sharing many kinds of eusocial behavior. Its somewhat larger colonies appear to be less stable over time. The species is found in Southern Africa.

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