

Damaraland and naked mole-rats: convergence of social evolution

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Introduction

African mole-rats (Family: Bathyergidae) have become well established as a model taxon with which to investigate the evolutionary origins and maintenance of cooperative breeding. They occupy an unusual position among vertebrates in having members whose breeding systems range from solitary to eusocial, defined by Michener (1969) and later generalized by Wilson (1971) as having overlapping generations, cooperative brood care, and reproductive division of labor. Following the first report of “eusociality” in naked mole-rats, *Heterocephalus glaber*, more than 30 years ago (Jarvis 1981), similar eusocial behavior was observed in Damaraland mole-rats, *Fukomys damarensis*, paving the way for phylogenetically controlled comparative studies (Bennett and Jarvis 1988; Jarvis and Bennett 1993).

The use of genetic techniques to reconstruct molecular phylogenies and reassess evolutionary relationships and biodiversity within the family has indicated that the Bathyergidae are an extensive adaptive radiation of subterranean rodents. Current estimates suggest that there are more than 30 species comprising six genera that range from strictly solitary to eusocial species, including the eusocial genus, *Heterocephalus* (with the monotypic naked mole-rat), solitary dwelling *Heliophobius*, *Bathyergus*, and *Georchus*, social *Cryptomys*, and social/eusocial *Fukomys* (Figure 19.1). Of particular significance to comparative studies is the fact that there have been convergent gains and losses of sociality within the family, which makes the Bathyergidae an excellent group with which to investigate the evolution of sociality and cooperative behavior. Given the phylogenetic reconstruction in Figure 19.1a, it is apparent that irrespective

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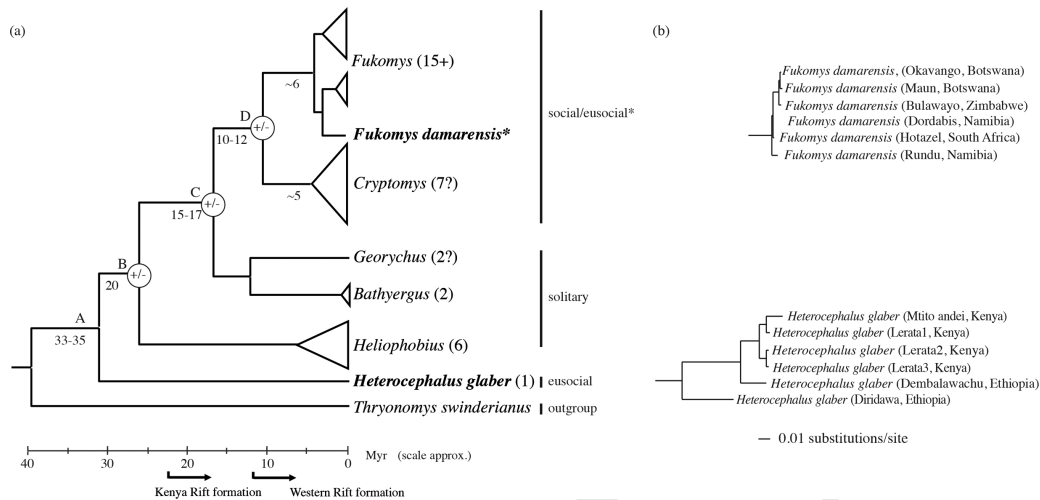


Figure 19.1. (a) Simplified phylogeny for the Bathyergidae indicating the six main clades/genera, together with the closest extant outgroup (the cane rat *Thyronomys swinderianus*), based on mitochondrial 12S rRNA and *cyt-b* sequence data. Numbers on internal nodes and scale bar represent divergence times in millions of years ago (Myr) estimated using a molecular clock approach, and using the Bathyergid fossil *Proheliophobius* for calibration of genetic distances. Numbers in parentheses indicate current estimates of species numbers in each genus. Circles with +/- at nodes represent common ancestors where sociality/a solitary lifestyle may potentially have been gained or lost, depending on the social status of the common ancestor of the family at node A. Further elaboration of social behavior is apparent along the *H. glaber* and *F. damarensis* lineages, and as a result they are often termed eusocial mammals. (b) *H. glaber* and *F. damarensis* clades sampled across their respective ranges, expanded to show the relatively deep branches of the former, compared with the shallow branches of *F. damarensis*, indicative of a recent radiation. Data and figure adapted from Faulkes et al. (1997a, 2004, 2010, 2011); Faulkes and Bennett (2013); Ingram et al. (2004).

of the status of the common ancestor of the family at Node A of the phylogeny, there have been phylogenetically independent gains and/or losses of social/solitary behavior and cooperative breeding at some or all of Nodes B, C, and D. In particular, naked and Damaraland mole-rats are highly divergent within the family, and it is likely that further social elaboration has occurred along their respective lineages, although on different timescales.

Heterocephalus is the basal lineage within the family and constitutes an ancient divergence, with the molecular phylogeny forming relatively deep branches among populations across its range. Molecular clock estimates of divergence times suggest that *Heterocephalus* separated from the common ancestor of the Bathyergidae more than 30 million

years ago (MYA), and fossils resembling naked mole-rats have been dated to approximately 18 MYA or earlier (Bishop 1962). Conversely, molecular phylogenies reveal that *F. damarensis* has small genetic differences and thus very shallow branches separating populations across the distributional range, indicating that the origin of the Damaraland mole-rat clade is much more recent, possibly within the last one million years (Van Daele et al. 2007). These differences in divergence between naked and Damaraland mole-rats are interesting in the context of the convergence of their social behavior (Table 19.1), and this chapter will compare and contrast both ultimate and proximate factors implicated in the evolutionary origin and proximate mechanisms of cooperative breeding and eusociality in these two species.

Table 19.1. Comparison of the characteristic features of the Damaraland mole-rat and the naked mole-rat

| | Damaraland mole-rat | Naked mole-rat |
|---|--|---|
| Habitat/rainfall/soil type | Arid; high temperatures (>28°C) and low irregular rainfall (ca. 200–400 mm annually); red Kalahari arenosols and a range of coarse sandy soils | Arid; high temperatures and low and irregular rainfall (ca. 200–400 mm annually); hard, consolidated, lateritic loams, sometimes fine sand, pure gypsum, and laterite |
| Burrow size (tunnel length) | 300m to 1km | 595m to 3.0km |
| Colony size range (mean) | 2 to ≥ 41 (12) | ≤ 10 to ≥ 290 (80) |
| Body size (mean) g | 100–281 (165) | 9–69 (34) |
| Reproduction | Obligate outbreeding; spontaneous ovulation; no seasonality; gestation 78 days, litters 1–5 (mean = 3) | Facultative inbreeding, but outbreeding preferred; spontaneous ovulation; no seasonality; gestation 72 days, litters 1–28 (mean = 11) |
| Reproductive skew/lifetime reproductive success | 1 female and 1–2 males; multiple paternity of litters possible; In a 5-year study, 92% of nonbreeding females never bred | 1 female and 1–3 males; multiple paternity of litters possible; 99.9% of >4,000 nonbreeders caught were re-caught as breeders |
| Extra-colony paternity | Yes | Unknown |
| Reproductive suppression | Clear physiological suppression in nonreproductive females only | Clear physiological suppression in nonreproductive females and males |
| Divisions of labor | Primary: reproductive Secondary: work related based on body size (foraging, defense, pup care) | Primary: reproductive Secondary: work related based on body size (foraging, defense, pup care) |

Distribution and geographical ecology

African mole-rats are widely distributed across sub-Saharan Africa, occurring from the extreme tip of the Cape region of South Africa through to disjunct and isolated populations in Southern Sudan in the north, Somalia in the east, and Ghana in West Africa. Over much of their range, speciation and diversity within the family appears to have been influenced by the physical, ecological, and climatic changes associated with the formation of the African Rift Valley, with cladogenesis associated with major episodes of volcanism (Faulkes et al. 2004, 2010, 2011).

In the Zambezian region of south-central Africa, shifting patterns of river drainage are of particular significance for populations of *Fukomys*, resulting in extensive vicariance and possible incipient speciation events (Van Daele et al. 2004, 2007). Within the family, the distributions of naked and Damaraland mole-rats are allopatric and geographically distant, but both are characterized by an arid habitat where rainfall can be unpredictable and typically averages no more than 200–400 mm per

year (Figure 19.2). Naked mole-rats are endemic to hot, dry regions of eastern Africa, encompassing much of Somalia, central Ethiopia, and parts of northern and eastern Kenya, extending south as far as the eastern edge of Tsavo West National Park. The soil types they inhabit are most frequently hard packed lateritic loams, although they may be found in fine sand, pure gypsum, and pure laterite (Hill et al. 1957; Jarvis 1985; Brett 1991a). Damaraland mole-rats are endemic to southern Africa, specifically the drier regions of northern South Africa, central and northern Namibia, Botswana, western Zimbabwe, and western Zambia; this is the widest distribution in southern Africa of any species of *Fukomys* or *Cryptomys*. Much of their distribution is characterized by red Kalahari arenosols, but they can also occur in a wide range of coarse sandy soils (Bennett and Jarvis 2004).

Burrow architecture

The disjunct occurrence of African mole-rats across their distributional range is predominantly determined

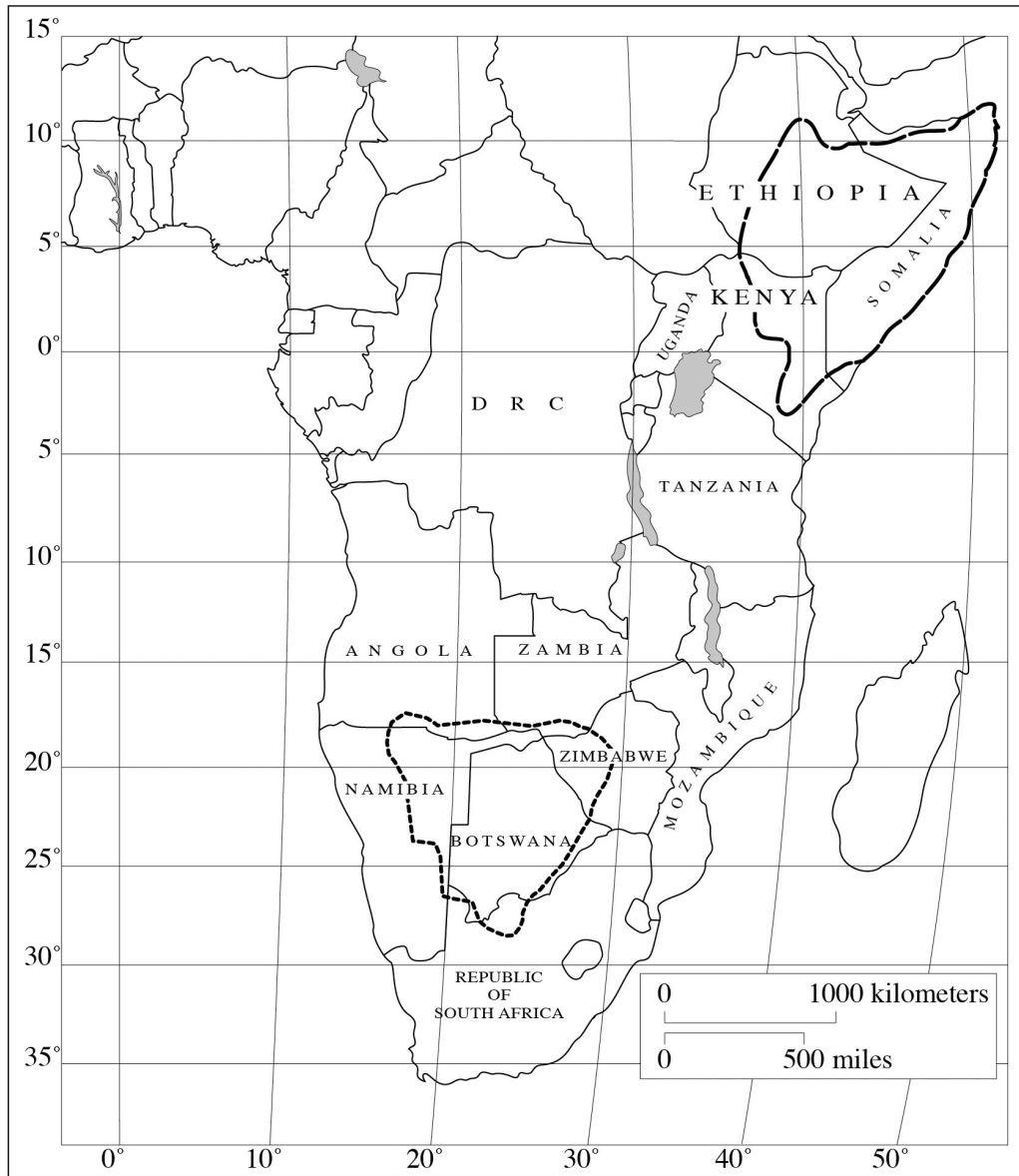


Figure 19.2. Map showing the approximate ranges of *H. glaber* (-.-.-) and *F. damarensis* (---).

Adapted from Bennett and Faulkes (2000).

by the presence of their principle food resource which comprises geophytes – plants with underground storage organs such as bulbs, corms, and tubers. Furthermore, the spatial pattern of these resources is thought to play a major role in shaping cooperative breeding and sociality. The distribution and size of geophytes dictates the overall burrow architecture, but there are a number of common features. Most of the burrow consists of superficial foraging tunnels that are excavated in search of food, and therefore occur at a depth of 5–25 cm (depth and chambers). Interspersed among these tunnels is a communal nest and toilet chambers that are up to 2.5 m in depth. Normally only one nest chamber is occupied at a time and these form important focal points where animals interact socially on a regular basis within the labyrinth of the burrow.

While the Damaraland mole-rat also has chambers that are used for food storage (where the food resources are small enough to gather), these are not found in naked mole-rat burrows, possibly because in the habitat of the latter the geophytes often form very large tubers that cannot be retrieved whole and stored. The food caches of the Damaraland mole-rat may represent resources that can be utilized by the queen when she is gravid and her mobility in the tunnel system is constrained. It is possible that they also represent a short-term emergency source of food to mitigate against periods of unsuccessful foraging. It has been calculated that the geophytes in the store may support a colony for a period of about 10 days (N. C. Bennett, unpubl. data).

Because of the difficulties involved in studying a subterranean animal, relatively few burrows have been fully mapped for either naked or Damaraland mole-rats. From those that have, it is apparent that they represent a considerable and largely permanent resource that is aggressively defended. Brett (1991a) radio-tracked individuals in a colony of 87 naked mole-rats and found that the total length of tunnels was 3–4 km, with 3,660–4,570 kg of soil being excavated in a single year, the equivalent of 2.3–2.9 km of new tunnels. These are impressive statistics for a rodent whose average body mass is 34 g.

Damaraland mole-rats are equally industrious, and while they occur in smaller groups, they are larger,

averaging 140 g in mass. During a two-week period that followed significant rainfall, a colony of 16 animals extruded 3,048 kg of soil, equivalent to approximately 1 km of tunnels (Jarvis et al. 1998). Clearly, rapid and dynamic changes to burrows in response to rainfall and food availability are possible in both species during the cooperative pursuit and exploration of the habitat for food resources, yet the central core of the burrow may remain static for many years if food remains available, and colonies of both Damaraland and naked mole-rats may occupy the same home range for many years (>6 and >7 years respectively; (Jarvis et al. 1998; Brett 1991b).

Thus, burrows represent a valuable, defensible, and long-term resource in terms of the food reserves contained within its range and as a safe nest site. This in itself may promote philopatry and the elaboration of sociality (Alexander et al. 1991). Aggression is apparent between adjacent colonies of naked mole-rats, and there is no evidence of adjacent colonies mixing, apart from occasional dispersers joining established colonies, although these may be rare occurrences (Brett 1991b; Braude 2000).

The importance of the burrow is further evidenced by an increased likelihood of survival in large established colonies. Of 21 nascent colonies of naked mole-rats containing 1–4 emigrants from nearby colonies, only one colony survived for longer than one year (O’Riain and Braude 2001). Similar observations have been made in Damaraland mole-rats: there are significant positive effects of group size on offspring recruitment and survival (A. J. Young et al. unpubl. data) and survival increases with group size (Jarvis et al. 1998).

Group size, composition, and divisions of labor

The establishment and maintenance of a large burrow system necessitates, or is at least facilitated by, large group size. Among cooperative breeders, African mole-rats are exceptional in this respect. In the naked mole-rat, colonies may range from as few as 10 to as many as 295 individuals, with an average of 75–80 animals per colony (Braude 1991, 2000; Brett 1991a).

Average biomass per colony is approximately 2.4 kg (for three complete colonies with over 50 individuals), while biomass ranged from 0.31–3.39 kg (with group sizes of 13 and 97, respectively) over 26 colonies from northern and southern Kenya (Brett 1991b). Group size in Damaraland mole-rats average 11 (range 2–41), with a modal size from 110 complete colonies of 12. Although the absolute numbers within a colony may be less than for naked mole-rats, the total biomass of animals is comparable at approximately 2 kg (Bennett and Jarvis 2004).

In both species large colony sizes are attained through natal philopatry arising from what appear to be the high risks and associated costs of dispersal. As a consequence, overlapping litters of nonbreeding individuals remain with their parents and adopt various helper roles, including cooperative care of the offspring of the breeding queen and 1–3 males (a reproductive division of labor), thereby fulfilling the definition of eusociality derived from social insects (Jarvis 1981; Brett 1991b; Jarvis and Bennett 1993). This characteristic reproductive division of labor within colonies, or reproductive skew, also translates into high skew in lifetime reproductive success (see “Nature and extent of reproductive skew”).

Arguably other mole-rat species may also meet the aforementioned basic conditions of eusociality, and there has been much debate about the usefulness of categorical definitions in this context (Bennett and Faulkes 2000; Burda et al. 2000). Unlike other species studied to date, however, both naked and Damaraland mole-rats exhibit a body size (and to some extent age) dependent behavioral division of labor among the nonbreeding helper cohort within the colony, with both sexes contributing equally to care of newborns and to maintenance and defense of the burrow system.

In Damaraland mole-rats, smaller individuals form a “frequent worker” group (Bennett and Jarvis 1988; Bennett 1990; Scantlebury et al. 2006). In newly established colonies, however, it is the larger animals in the colony that constitute the work force (Gaylard et al. 1998). In naked mole-rats, the frequency of work described as colony maintenance, including foraging for food, digging, and maintaining the burrow system, shows a negative trend with increasing body mass.

Nonbreeders also huddle with pups, handle and groom them, retrieve them if they wander out of the nest, and evacuate them during disturbances, and again small (usually younger) animals are the most active in pup care.

Conversely, defense-related activities such as guarding and patrolling increase in frequency with body mass (Faulkes et al. 1991a; Lacey and Sherman 1991), and larger individuals are the most active “volcanoers,” producing the molehills (Braude 1991). This is a risky activity as animals are potentially exposed to predators when near the surface. Individuals gradually switch from maintenance to defense activities as they age and grow larger. However, a strict age polyethism may frequently be obscured by behavioral and body size changes associated with variation in colony composition and within-colony competition to fill reproductive vacancies (Lacey and Sherman 1991, 1997). For example, individuals born to mature colonies may remain small and therefore maintain their role as frequent workers for many years, whereas individuals born in nascent colonies attain a higher body mass more rapidly and move out of the worker role to become defenders, dispersers, or, more rarely, breeders (O’Riain and Jarvis 1998). Thus, although the largest individuals in a naked mole-rat colony are usually the oldest, early social influences can affect growth rates and hence the precise role an individual occupies in the colony’s work force.

Although morphological caste determination is rare in mammals, there is evidence for a male disperser morph in naked mole-rats (O’Riain et al. 1996; Braude 2000), and naked mole-rat queens exhibit morphological differences in their vertebrae compared to workers (O’Riain et al. 2000). In the Damaraland mole-rat, breeding females are also morphologically different from the nonbreeding females within a colony (Young and Bennett 2010), and physiological castes are also discernable (Scantlebury et al. 2006). Regarding the latter, during the dry season larger “infrequent workers” have lower metabolic rates than “frequent worker” colony members. During the wet season, however, there are no differences. This implies that larger mole-rats become physiologically distinct and more active prior to dispersal. Physiological differences have also been

recorded in naked mole-rats, in which disperser males have reproductive hormones that resemble those of breeder males. Table 19.1 summarizes and compares some of the social and reproductive characteristics for both species.

Ultimate factors shaping social evolution

As an explanation for sociality in the Bathyergidae, the “aridity food distribution hypothesis” (AFDH) has received much attention. The AFDH is specific version of the ecological constraints hypothesis, and posits that increased natal philopatry, cooperative breeding, and ultimately eusocial behavior in African mole-rats have evolved in response to patterns of rainfall and their interaction with the geology and vegetation of habitats occupied by this group of organisms. Rainfall affects soil hardness and therefore the energetics of burrowing, and importantly also influences the patterns of mole-rat food distribution and the subsequent costs and risks of foraging and dispersal (Bennett 1988; Lovegrove and Wissell 1988; Lovegrove 1991; Jarvis et al. 1994, 1998). In arid habitats it is easy to see how sociality and cooperation could be adaptive, as cooperative foraging divides the energetic costs of burrowing and increases the chances of finding food in the form of underground roots and tubers. The clumped nature of these geophytes and, in some cases, their large size once found, are sufficient to provide the energy needed to sustain large groups of animals.

Empirical evidence from the field in support of the AFDH comes from both inter- and intraspecific studies across the family. Interspecifically, phylogenetically controlled comparative analysis of the Bathyergidae reveal a significant positive correlation between social group size and the coefficient of variation in rainfall, while mean distances between food sources and numbers of months in which rainfall exceeds 25 cm, the amount required to penetrate to the depth of foraging tunnels, are inversely correlated with colony size, as predicted by the AFDH (Faulkes et al. 1997a).

Analyses of the architecture of burrow systems demonstrates that in the arid habitats inhabited by naked and Damaraland mole-rats, colonies containing larger

numbers of individuals are able to explore their habitat and search for food more efficiently with a greater degree of complexity (calculated as fractal dimension) of the foraging tunnels than smaller groups (Le Comber et al. 2002). Furthermore, a long-term field study of Damaraland mole-rats has shown that larger colonies are less likely to fail when environmental conditions are at their most extreme and challenging, such as during droughts, again emphasizing the adaptive advantage of sociality (Jarvis et al. 1998).

The prediction of AFDH that increased aridity should reduce dispersal and increase within-group relatedness (R) has also found support. Hess (2004) used microsatellite genotyping to estimate relatedness in colonies across an aridity gradient in Kenya, finding a weak but statistically significant positive correlation in support of the hypothesis that aridity constrains dispersal. Similarly, comparison of intracolony relatedness in Damaraland mole-rats revealed, as predicted, a lower R -value at a field site in Hotazel, South Africa, compared to a more arid site at Dordabis, Namibia (mean \pm 95% confidence interval: 0.40 ± 0.02 versus 0.54 ± 0.04 respectively; Burland et al. 2002).

Intraspecific comparisons of philopatry and dispersal in arid and mesic-dwelling common mole-rats (*Cryptomys hottentotus*), a sister clade to *Fukomys* found in South Africa, have also shown that immigration and emigration were lower at an arid site than at a mesic one, indicating that constraints on dispersal are higher in areas of low and unpredictable rainfall (Spinks et al. 2000). Despite these differences, however, estimates of intracolony relatedness were not found to differ between sites (mean \pm standard error [S.E.] = 0.23 ± 0.02 at Somerset West, South Africa (mesic site) vs. 0.28 ± 0.03 at Steinkopf, South Africa, an arid site).

While the aforementioned studies offer support for the AFDH as a means of understanding the ecological drivers of mammalian eusociality, these environmental factors are operating within the context of life history traits that facilitate cooperative breeding. Clearly an ancestral tendency for monogamy and the ability to form social bonds, a subterranean lifestyle that constrains dispersal, and longevity are all vital prerequisites for social elaboration and cooperation in kin groups (Burda et al. 2000; Lukas and Clutton-Brock 2012).

Proximate factors maintaining high reproductive skew and cooperative breeding

The nature and extent of reproductive skew

In colonies of all cooperatively breeding mole-rats studied to date, a single female – the queen – normally breeds with one, and rarely two or three resident breeding males. This indicates that at any one point in time within a colony, all social mole-rat groups have extreme reproductive division of labor and high reproductive skew among females, with somewhat lower skew among males. "Snapshot" data such as this can be misleading, however, and it is important to consider a temporal component, since skew in terms of lifetime reproductive success (LRS) can differ considerably among species depending on the chances of dispersal and independent breeding.

The AFDH predicts that skew in LRS will be greater in species such as naked and Damaraland mole-rats, which inhabit harsher habitats where ecological constraints are higher. In such habitats, while individual reproduction may be prevented over relatively long time periods, longer lifespans may allow mole-rats to breed during periods when environmental pressures on individual reproduction are relaxed.

In Damaraland mole-rats, 89% of 18 colonies had just one breeding male resident at any particular time (Burland et al. 2004). These individuals can be readily distinguished by morphological characteristics as well as paternity analysis. In more than half (53% of 17 colonies), however, no father could be assigned to at least one of the resident offspring. This indicates that the breeding female has contact with other non-resident males either by temporarily leaving the colony, or more likely by transient males passing through the colony. Given that plural breeding among female Damaraland mole-rats has not been observed, either in captivity or in the wild, skew in lifetime reproductive success among males appears to be potentially much less than in females. In the longer term, estimates from a mark-release-recapture study in Namibia have revealed that over a five-year period, 370 of 403 (92%) of nonbreeding females did not breed at all (Jarvis and Bennett 1993; Jarvis et al. 1994).

Very high skew in both the short-term and long-term is also found in naked mole-rats. In captive colonies of naked mole-rats up to three males can mate with the queen (Lacey and Sherman 1991), and molecular analyses confirm that up to three males may sire offspring in a single litter (Faulkes et al. 1997b). Unlike in Damaraland mole-rats, plural breeding has been found in both captive and wild colonies, although it is apparently rare. For example, Braude (1991) recorded only two instances of plural breeding from an extensive field study of 2,051 naked mole-rats from 23 colonies in Meru National Park, Kenya, and only a single breeding queen was detected in wild colonies in Kenya studied by Brett (1991b) and Jarvis (1985).

In captivity, Jarvis (1991) reported groups containing two queens but offspring produced were rarely reared successfully and often there was intense conflict between the breeding females. She also reported that in some of these captive colonies, plural breeding followed periods of high offspring recruitment and suggested that in the wild, such favorable environmental conditions may trigger dispersal of rival females and new colony formation. Overall, skew in LRS in naked mole-rats is even more extreme than in Damaraland mole-rats, with fewer than 0.1% of over 4,000 recaptured nonbreeders eventually becoming queens (Jarvis et al. 1994).

Kin structure of colonies, reproductive suppression and reproductive skew

Of the social mole-rats in the genera *Cryptomys* and *Fukomys* studied to date, both in the wild and in captivity, all appear to have a mating system that involves obligate outbreeding. Hence a colony of social mole-rats comprised of parents and offspring will by default exhibit a reproductive division of labor and high reproductive skew simply as a result of there being no unrelated mates accessible for adult offspring of breeding age. This effect is so strong that in both wild and captive colonies of Damaraland mole-rats in which the breeding female has died, all individuals will remain reproductively quiescent, sometimes for years, until a new, unrelated, individual becomes available, or until fragmentation of the colony occurs (Jarvis and Bennett

1993; Rickard and Bennett 1997; Bennett et al. 1996; Bennett and Faulkes 2000).

In contrast, naked mole-rats have been shown to adopt a mating strategy of facultative inbreeding: the incest avoidance mechanisms observed in *Cryptomys* and *Fukomys* are not present, and if no suitable unrelated mates are available, mating with close relatives within the colony may readily occur. These incestuous tendencies may be an adaptive trait enabling reproduction to continue when environmental conditions prevent dispersal and outbreeding, and were originally proposed as an important factor in explaining eusociality by Reeve et al. (1990), who argued that inbreeding produces a within-kin-group genetic structure analogous to haplodiploidy in the Hymenoptera. Specifically, Reeve et al. (1990) estimated intracolony relatedness in some groups at 0.8, a value greater than the average 0.75 relatedness in haplodiploid organisms where the queen is singly mated (Faulkes and Bennett 2009). The observation of normal familial levels of relatedness in Damaraland mole-rats, however, argues against high relatedness per se as a prerequisite for the emergence of eusociality (Burland et al. 2002).

The contrasting mating patterns of inbreeding and outbreeding among the social mole-rat genera provide insight into species differences in the proximate control of reproductive skew. Molecular genetic studies combined with mark-release-recapture data from *Cryptomys* and *Fukomys* show that intergroup movements may be common, giving rise to the potential for reproductive conflict between the breeding and nonbreeding members of the colony (Burland et al. 2004; Bishop et al. 2004). In Damaraland mole-rats, immigrants of both sexes were identified and opposite-sex nonbreeding animals were present at the same time in some colonies (Burland et al. 2004). Nonetheless, only a single queen was found to be breeding, begging the question of what proximate factors prevent these unrelated nonbreeding animals from reproducing.

In such cases, inbreeding avoidance alone is not sufficient to explain skew. In the case of females, the proximate mechanism driving skew is a physiological block to reproduction in the form of disruption of gonadotrophin releasing hormone (GnRH), leading ultimately to a failure to ovulate (Bennett et al. 1996,

1999; Molteno and Bennett 2000). Curiously, in female Damaraland mole-rats there are no differences in the number, morphology, or size of the cell bodies of the GnRH neurosecretory cells between reproductive and nonreproductive female Damaraland mole-rats (Molteno et al. 2004). There is, however, a significant difference in the amount of GnRH that is retained in the hypothalamic neurosecretory cells of these two groups, with GnRH concentrations in the median eminence and proximal pituitary stalk significantly higher in nonreproductive compared to reproductive females. These findings imply that the GnRH release is physiologically inhibited in nonreproductive females and accumulates in the cells, leading to the observed increase in GnRH concentrations. Such an inhibition mechanism could be favored by the fitness costs of attempting to breed in the presence of a more dominant, reproductive individual.

The social cues that lead to the suppression of GnRH and subsequent state of anovulation in Damaraland mole-rats remain unknown, since in captivity this species is typically kept in family groups where incest avoidance maintains skew; behavioral interactions between unrelated nonbreeding adults have not been studied. Nonbreeding males are not physiologically suppressed to the same extent as females, but they do possess increased proportions of sperm with morphological defects (Maswanganye et al. 1999), although the significance of these abnormalities for fertility is unclear. Furthermore, in contrast to females, the mean concentration of GnRH in the hypothalamus of reproductive and nonreproductive male Damaraland mole-rats is similar (Molteno et al. 2004).

Among cooperative breeders, naked mole-rats exhibit the most extreme of socially induced infertility, with nonbreeders of both sexes being physiologically suppressed in the presence of the dominant queen. In females, gonadal development is much less than that observed in nonbreeding Damaraland mole-rats, leaving them in an apparent prepubertal state with gonads almost embryonic in appearance. As in Damaraland mole-rats, ovarian cyclicity and ovulation are ultimately blocked.

In male naked mole-rats, most nonbreeders have spermatozoa within the reproductive tract, but they

are both reduced in number and lack normal levels of motility. In both sexes, these gonadal deficiencies appear to arise from reduced secretion of luteinizing hormone (Faulkes et al. 1990a, 1990b, 1991a, 1991b; Faulkes and Abbott 1991).

While incest avoidance, together with other factors, may explain how reproductive division of labor is maintained in Damaraland mole-rats, the proximate control of reproductive skew in naked mole-rats is mediated through dominance: the extreme (but potentially rapidly reversible) reproductive blocks are brought about specifically by behavioral contact with the dominant breeding queen (Faulkes and Abbott 1993; Clarke and Faulkes 1997, 1998; Smith et al. 1997). Why have subordinate naked mole-rats evolved to “accept” such extreme physiological suppression of reproduction? High reproductive skew and a large nonbreeding workforce are clearly adaptive in this species. Facultative inbreeding occurs both in captivity and in the wild (Faulkes and Bennett 2009), largely due to ecological constraints that preclude dispersal and result in a near zero chance of encountering an unrelated mating partner. In the face of within-colony competition to mate, a control mechanism has evolved whereby social cues bring about suppression of reproductive physiology in both sexes. Without such suppression, reproductive conflict among related individuals attempting to breed would likely be rampant by opting out subordinates likely avoid costly competition. Debate continues with respect to the extent to which suppression is “imposed” (dominant control) or “accepted” (so called self-restraint), and how these concepts fit into theoretical models of optimal reproductive skew. Within this discussion it is important to consider mechanistically how suppression is mediated, irrespective of the relative costs and benefits of suppression to the subordinate nonbreeder. For example, it is possible to understand a dominant control model in the context of stress physiology, but more difficult to explain how a restraint model may operate from a neuroendocrine or physiological point of view (Faulkes and Bennett 2009).

Among other species of African mole-rats, including the common, Mashona, and giant mole-rats, no physiological suppression of reproduction is observed

(Bennett et al. 1997; Bennett et al. 2000; Spinks et al. 2000). In these taxa, opportunities for individual reproduction following dispersal are apparently greater and incest avoidance alone is apparently sufficient to maintain reproductive skew within colonies. The Damaraland mole-rat is intermediate between these species and the naked mole-rat, with suppression of reproductive physiology restricted to nonbreeding females (Bennett et al. 1996; Molteno et al. 2004). A possible explanation is that this trait may have evolved as a result of reproductive conflict as a potential control mechanism by the queen preventing unrelated immigrant males from mating with other females in the colony, thus maintaining the high skew observed among females.

The neurobiology of living together

A critical but until recently largely overlooked proximate factor driving sociality in African mole-rats is the ability to modulate tolerance and social affiliation among both breeding and nonbreeding animals within a colony. Not all mole-rat species have this trait, as the solitary species are highly aggressive toward one another, pairing only briefly to mate, with young being expelled from the natal burrow immediately after weaning (Bennett and Jarvis 1988; Bennett et al. 1991). Among mammals generally, the evolution of cooperative breeding is restricted to socially monogamous species (Lukas and Clutton-Brock 2012) in which pair-bonding behavior is dependent on particular neurobiological phenotypes (Young and Wang 2004).

In rodents, two neuropeptides, oxytocin (OXT) and vasopressin (AVP), act centrally in the brain to modulate sociality, pair bonding, and aggression (Lim and Young 2006). More specifically, the location, pattern, and density of receptors for OXT and AVP differ significantly between promiscuous and monogamous species of voles (*Microtus montanus* and *M. ochrogaster* respectively) and mice (*Peromyscus* spp.; Curtis et al. 2007). Recent studies have determined that the naked mole-rat exhibits higher levels of OXT receptor binding than the solitary and promiscuous Cape mole-rat (*Georchus capensis*) in several significant regions of

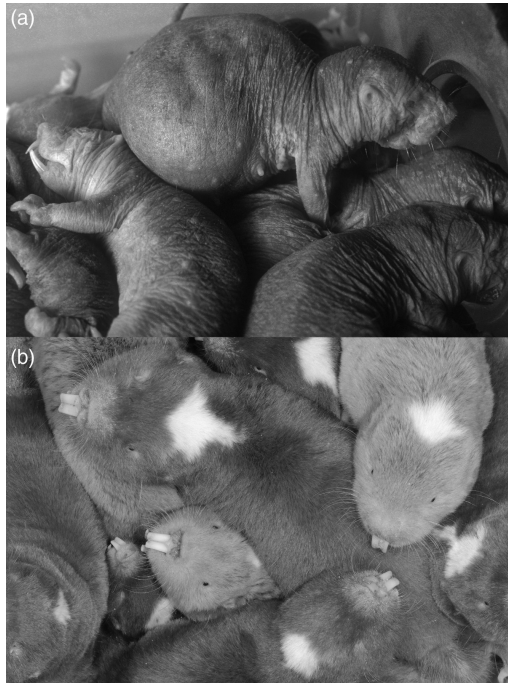


Figure 19.3. (a) Naked mole-rats huddling in a nest chamber. The pregnant queen is on top of the pile of animals, and below her two large animals guard one entrance to the nest. (b) Damaraland mole-rats in a nest chamber. Photographs by C. Faulkes and T. Jackson. See plate section for color figure.

the forebrain. As with social voles, OXT receptor levels in naked mole-rats are intense and extensive in an area known as the nucleus accumbens. Conversely, OXT receptors are not detectable in the Cape mole-rat in this area, consistent with a paucity of prosocial behaviors exhibited by this species (Kalamatianos et al. 2010).

The interpretation of these findings is that abundance of OXT receptor densities in the nucleus accumbens of naked mole-rats reflects their high levels of sociality, alloparenting behavior, and potential for reproductive pair bonding. As the queen may have up to three male consorts with which she mates during a particular estrus period, the mating system is polyandrous rather than monogamous, but bonding is nonetheless simultaneous and long-term, rather than sequential. In that sense it resembles the bonds

that form in a monogamous relationship. Preliminary studies confirm that the Damaraland mole-rat, which is convergently social (Figure 19.3), resembles both naked mole-rat (and social voles), with OXT receptor binding being present in the nucleus accumbens (Coen et al. 2011).

Conclusions

Within the extensive adaptive radiation of African mole-rats endemic to sub-Saharan Africa, naked and Damaraland mole-rats are two key species divergent within the family, but convergent in their highly social cooperative breeding behavior. As well as revealing possible gains and losses of sociality across the family, molecular phylogenies have enabled comparative analyses and the investigation of the ultimate drivers and proximate maintenance of social behavior. Such studies indicate that sociality and cooperative breeding require the correlated evolution of a mosaic of characteristics, set against a backdrop of phylogenetically constrained life-history traits such as a subterranean lifestyle and relatively long lifespan. These include the appropriate neurobiological phenotype facilitating the ability to form social bonds followed by a number of behavioral and reproductive adaptations including inbreeding avoidance, behavioral division of labor, and socially induced suppression of reproduction.

Ultimately the social lifestyle of mole-rats is driven by natal philopatry, most likely imposed by the high costs of dispersal and the risks involved in foraging singly or in small groups where food resources are dispersed. These problems become exaggerated in arid habitats such as those exploited by naked and Damaraland mole-rats, where the soil is also compact and energetically costly to excavate. Under these conditions the best strategy is to stay and help, delaying breeding rather than attempting to increase individual fitness.

This reproductive cost is offset by gains in inclusive fitness, as the majority of colony members are closely related (Reeve et al. 1990; Faulkes et al. 1997b; Burland et al. 2002). Given the prevalence of natal philopatry and sociality across the family, and the advantages of

such behavior, a major question is: why have some species gained a solitary and aggressive phenotype along with its underlying neurobiology or, alternatively, lost the social phenotype? Perhaps relatively common mutations occurring in a few key genes underlie the pair-bonding observed in the social phenotype. These may be under strong selection in certain habitats, but neutral in others, and thus lost relatively easily.

Although convergence within the family has produced similar social phenotypes in naked and Damaraland mole-rats, identifying the similarities and differences in the underlying proximate mechanisms are of interest in understanding common mechanisms and neurobiological substrates that underpin behavior. Whether the differential expression of such mechanisms in asocial and social African mole-rats is structured genetically, in a similar way to that seen in voles, remains a fascinating question that still requires answering.

Adaptations to the subterranean niche have not only given rise to sociality, but also to a host of unexpected traits that have become of great interest to researchers into human health. In naked mole-rats, these include extreme longevity and lack of senescence (Sherman and Jarvis 2002; Buffenstein 2008), insensitivity to certain kinds of pain (Park et al. 2008; Smith et al. 2011), and resistance to cancer (Kim et al. 2011; Yu et al. 2011; Tian et al. 2013). Future research in African mole-rats will likely focus on understanding these adaptations, which are unique and of general interest. Their discovery through basic, exploratory research is significant, and future explorations stand to gain much by integrating evolutionary theory with exploration of these interesting, applied, research contexts.

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