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Phil. Trans. R. Soc. B 2013 **368**, 20120347, published 8 April 2013

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Review

Cite this article: Faulkes CG, Bennett NC. 2013 Plasticity and constraints on social evolution in African mole-rats: ultimate and proximate factors. *Phil Trans R Soc B* 368: 20120347.
<http://dx.doi.org/10.1098/rstb.2012.0347>

One contribution of 15 to a Theme Issue 'Flexibility and constraint in the evolution of mammalian social behaviour'.

Subject Areas:

evolution, ecology, behaviour

Keywords:

Bathyergidae, social evolution, cooperative breeding, African mole-rat, reproductive skew, eusociality

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Plasticity and constraints on social evolution in African mole-rats: ultimate and proximate factors

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Here, we review comparative studies of African mole-rats (family Bathyergidae) to explain how constraints acting at the ultimate (environmental) and proximate (organismal) levels have led to convergent gains and losses of sociality within this extensive adaptive radiation of subterranean rodents endemic to sub-Saharan Africa. At the ultimate level, living in environments that range from mesic through to arid has led to both variation and flexibility in social organization among species, culminating in the pinnacle of social evolution in the eusocial naked and Damaraland mole-rats (*Heterocephalus glaber* and *Fukomys damarensis*). The common mole-rat (*Cryptomys hottentotus*) provides a model example of how plasticity in social traits exists within a single species inhabiting areas with different ecological constraint. At the proximate level, reproductive strategies and cooperative breeding may be constrained by the correlated evolution of a suite of traits including physiological suppression of reproduction, the development of physiological and morphological castes, and the mode of ovulatory control and seasonality in breeding. Furthermore, recent neurobiological advances indicate that differential patterns of neurotransmitter expression within the forebrain may underpin (and limit) either a solitary or group living/cooperative lifestyle not only in mole-rats, but also more widely among disparate mammalian taxa.

1. Introduction

Within Mammalia, rodents are an excellent taxon with which to investigate the dynamic nature of social behaviour; they are the largest mammalian order consisting of more than 2000 species, occurring in all the main habitats on every continent except Antarctica. Their diverse social and reproductive systems, but relative ease of studying in the wild and captivity often make them a model system of choice for hypothesis testing of the proximate mechanisms, and ultimate causation of a range of behavioural phenomenon [1].

African mole-rats of the family Bathyergidae form the largest of the extant African (Phiomorph) families in the rodent suborder Hystricomorpha. Since the discovery of eusociality in the naked mole-rat (*Heterocephalus glaber*) by Jarvis [2], there has been increasing interest in the family as a model mammalian system for understanding/unravelling the evolution and maintenance of vertebrate sociality and cooperative breeding. Jarvis adopted the definition of eusociality derived for social insects, i.e. species having a reproductive division of labour, overlapping generations and cooperative care of young. The unusual characteristics exhibited by naked mole-rats and other bathyergids result from adaptations to the extreme demands of the subterranean niche, culminating in the unique 'insect-like' social system of the former. A mole-rat living underground as part of a complex cooperatively breeding society requires a suite of neurobiological and physiological specializations imposed by the constraints that this lifestyle demands, while retaining some flexibility to respond to environmental changes (e.g. variation in rainfall and food supply). These specializations may differ markedly among mole-rat species, because some taxa have adopted a strictly solitary lifestyle, and lack social tolerance and the ability to form long-term social bonds. Thus, across the family Bathyergidae, at the species level plasticity in the response to exploiting the subterranean niche has resulted in a wide spectrum

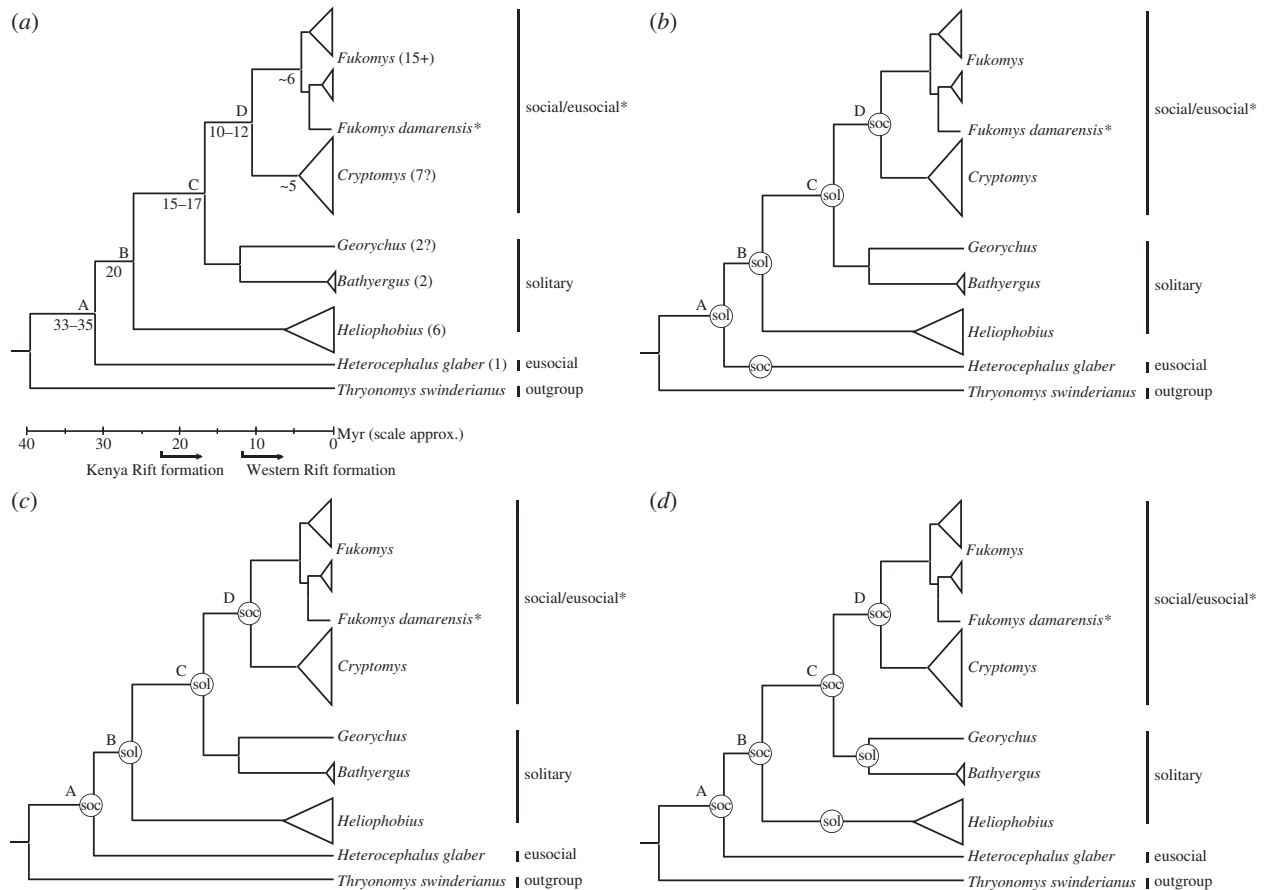


Figure 1. (a) Simplified phylogeny for the Bathyergidae indicating main clades/genera, together with the closest extant outgroup, the cane rat *Thryonomys swinderianus*, and based on mitochondrial 12S rRNA and cytochrome b sequence data. Numbers on internal nodes represent divergence times in millions 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. (b–d) Represent alternative hypotheses for convergent gains and losses in solitary/sociality, dependent on the status of the common ancestor of the family: (b) with a solitary common ancestor, sociality arises independently twice in *Heterocephalus* and the common ancestor of *Fukomys*/*Cryptomys*, with further elaboration to eusociality in extant *H. glaber* and *F. damarensis*; with a social common ancestor, either sociality is lost in the common ancestor of *Heliophobius* and descendent lineages to re-emerge in *Fukomys*/*Cryptomys* (c), or retained in common ancestors with loss and the evolution of a solitary lifestyle in lineages leading to *Heliophobius*, *Bathyergus* and *Georychus* (d). Other, less parsimonious explanations are also possible (data adapted from earlier studies [3–8]).

of social organization (from solitary to eusocial). However, at the extremes of this spectrum, specialization may restrict intraspecific flexibility in social structure, especially for the solitary species where neurobiological factors and the resultant behaviours may preclude sustained group living.

In this review, we will consider how living in environments that range from mesic through to arid has led to variation in social organization among African mole-rat species through convergent gains and losses of traits. We will discuss how, at the proximate level, reproductive strategies and cooperative breeding may be constrained not only by neural substrates, but also by the correlated evolution of a suite of other traits, including physiological suppression of reproduction, the development of physiological and morphological castes, and the mode of ovulatory control and seasonality in breeding.

2. Background: phylogeography and distribution

African mole-rats represent an extensive adaptive radiation of subterranean rodents across sub-Saharan Africa. A recently revised estimate of biodiversity in the family suggests 30 or more species comprising six genera: eusocial *Heterocephalus*

(with the monotypic naked mole-rat), solitary dwelling *Heliophobius*, *Bathyergus* and *Georychus*, social *Cryptomys* and social/eusocial *Fukomys* (figure 1a) [3–8]. Mole-rats may be found from the Cape region of South Africa through to disjunct 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 appear 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 [4–6]. Additionally, shifting patterns of drainage evolution are of particular significance for populations of *Fukomys* in the Zambezi region of South-Central Africa, resulting in extensive vicariance and possible speciation events [8,9].

Over this wide distributional range mole-rats inhabit a variety of soil types in different biomes and climatic zones, and some general trends are evident. First, as they feed exclusively on underground roots and tubers, this is the overriding constraint on their distribution—for example, they are not found in heavily forested regions or in extreme deserts. Second, solitary mole-rats (*Heliophobius*, *Bathyergus* and *Georychus*) are mainly restricted to mesic regions of higher rainfall (with a moderate and predictable pattern of

precipitation greater than 400 mm per annum). The social genera (*Cryptomys* and *Fukomys*) are found in both mesic and xeric (low and unpredictable rainfall of less than 400 mm per annum) regions. *Heterocephalus* occurs exclusively in the xeric regions of East Africa (parts of Kenya, Ethiopia and Somalia). On average, the arid regions inhabited by mole-rats may have only four months per year having more than 25 mm of rain (approximately the quantity required to soften the soil at the depth of foraging tunnels and thus facilitate burrowing) [10]. This association between the distribution of extant species with different social phenotypes and ecological constraints has led to formulation of the aridity food distribution hypothesis (AFDH) as an ultimate explanation for the evolution of sociality in the Bathyergidae (see §4 below).

3. Inferring convergent gains and losses of sociality

Before embarking on a detailed discussion of the AFDH and ultimate drivers of social evolution in the Bathyergidae, it is important to consider the occurrence of sociality and cooperative breeding within an evolutionary context, and thus enable a comparative phylogenetic approach to understanding their social evolution. Figure 1*b–d* illustrates three possible scenarios that would explain the observed pattern of sociality across the genera, varying according to what the social status of the common ancestor of the family was (node A in figure 1). Inferences may be made by extending the phylogeny to also consider the status of the extant Phiomorph outgroups of the Bathyergidae, which are dassie rats (Petromuridae), cane rats (Thryonomyidae) and Old World porcupines (Hystriidae). While detailed studies on the socio-biology of these taxa are sparse, the close outgroup *Petromus typicus* (the dassie rat) is reported to exhibit social monogamy forming strong social bonds, low levels of inter-generational aggression and paternal care [11]. Phylogenetic character mapping to reconstruct ancestral states within the Bathyergidae gives ambiguous results, with likelihood and maximum-parsimony approaches producing equivocal states for the ancestors at nodes A, B and C in figure 1. What is unequivocal is that irrespective of the status of the bathyergid common ancestor at node A, there have been convergent gains and losses of sociality within the family (figure 1*b,c*), presumably in response to changing environmental pressures (ultimate factors), such as climate change and tectonics.

4. Ultimate factors: an ecological constraints model for social evolution

The subterranean niche confers a number of advantages, such as protection from predators and buffering of thermal extremes. In terms of predation and predator avoidance itself being a driver for social evolution in the Bathyergidae, it is not thought that these play a major role as causative factors because predators ('mole-snakes' and birds of prey) are prevalent across all mole-rat habitats, yet levels of sociality differ. Despite the advantages, there are also considerable costs and constraints associated with living underground: dispersal and new burrow formation may be costly as digging through soil is energetically expensive, perhaps up to 3600 times that of surface locomotion [12]. Costs of

burrowing may vary with soil hardness and moisture content [13], which may in turn vary among different habitats, or within a habitat between the seasons (e.g. before and after rains). It is these ultimate constraints that are hypothesized as drivers of social evolution in African mole-rats.

All African mole-rats feed on underground roots and tubers (geophytes) and *Bathyergus* may also supplement its diet with above-ground forbes and grasses, which are encountered by digging foraging tunnels from the central core of the burrow system (for review see [14]). The distribution of these roots and tubers eaten by mole-rats varies with habitat. In mesic regions, these food resources are more uniformly distributed, whereas in xeric regions of low or unpredictable rainfall, the plants are arid-adapted and more widely dispersed, or occur in high-density clumps that are widely dispersed and patchily distributed. The AFDH brings together these environmental constraints as an explanation for social evolution in the Bathyergidae (figure 2). It posits that increased natal philopatry leading to cooperative breeding, and ultimately eusocial behaviour in African mole-rats may have evolved in response to the unpredictable rainfall patterns of the habitat, its effects on their food distribution, and the resulting costs and associated risks of unsuccessful foraging, dispersal and new colony formation [3,10,15–18]. In such a scenario, sociality would be adaptive, as cooperative foraging and burrow maintenance distributes the energetic costs of burrowing among colony members and increases the probability of finding food. The clumped nature of the geophytes and, in some cases, their large size, ensures that these resources are potentially sufficient to sustain large groups of animals. The AFDH is dependent on individuals having all the necessary neurological substrates in place to facilitate social tolerance, extended periods of philopatry and thus group living and ultimately cooperative behaviour. Thus, populations of mole-rats that are subject to changing climate (for example aridification) or that are expanding from mesic into more arid environments will be under strong selection for genotypes that give rise to social phenotypes. An increasing body of work is now identifying candidate genes and the mutations that may underpin differences in the expression of social behaviour within and among species (see §5 below).

Support for the AFDH playing at least a role in the evolution of sociality comes from both inter- and intraspecific studies across the Bathyergidae. A phylogenetically controlled comparative analysis of data from across the family revealed significant relationships as predicted by the AFDH between social group size and geophyte density, the coefficient of rainfall variation and the mean number of months per year where rainfall exceeded 25 mm. Interspecific analyses of burrow geometry using calculations of fractal dimension clearly demonstrate that in arid habitats, colonies containing larger numbers of individuals are able to explore their habitat more effectively with a greater degree of complexity of the foraging tunnels than smaller groups [19]. In addition, studies of burrow geometry within a single social species (*Fukomys mechowii*) further support the AFDH, where burrow fractal dimension increased with colony size and was higher during the wet season than during the dry season [20]. Furthermore, a long-term field study of eusocial Damaraland mole-rats has shown that larger colonies are more likely to survive when environmental conditions are at their most extreme (as observed during an extended period of drought), again emphasizing the adaptive advantage of sociality [18].

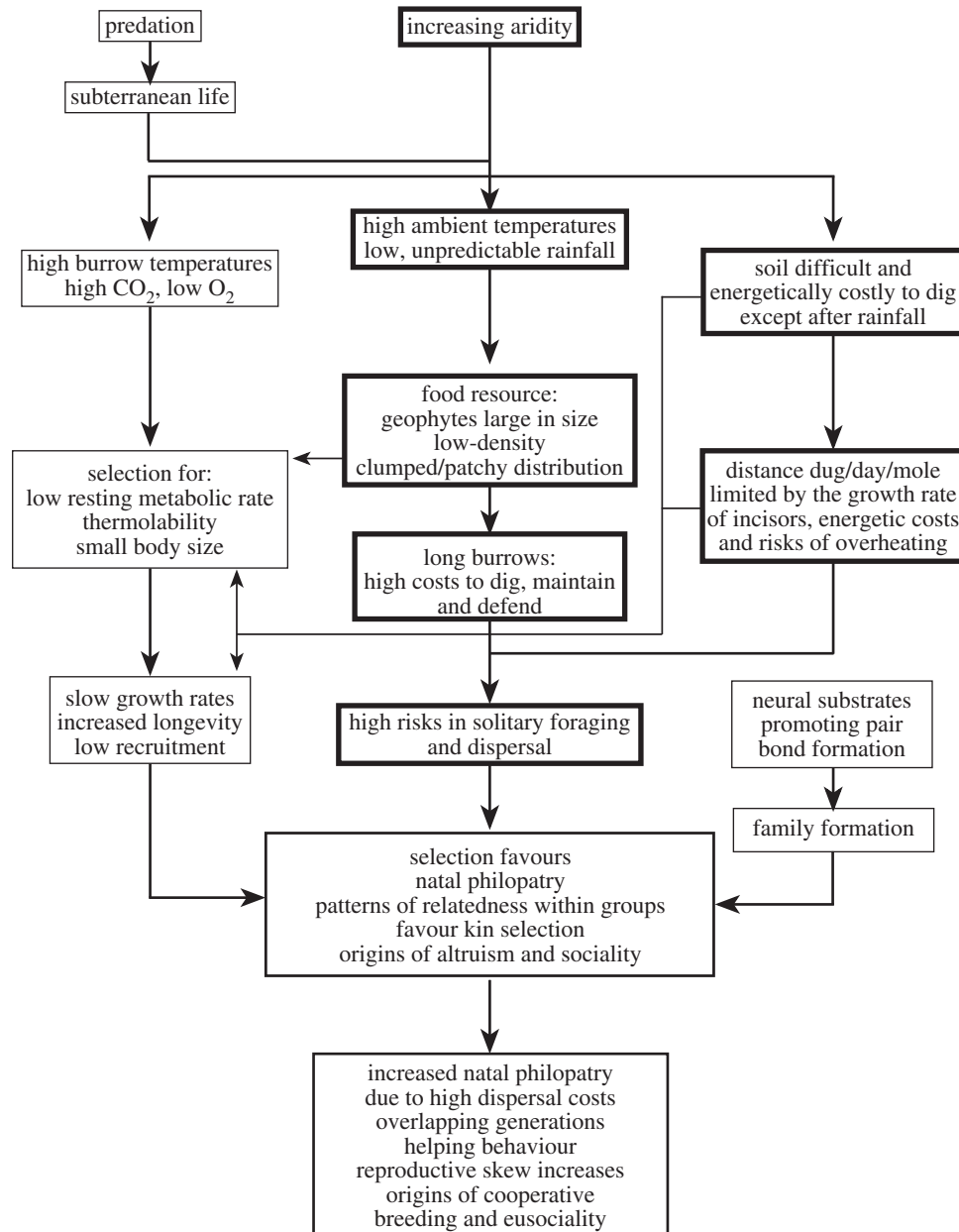


Figure 2. Summary of the ultimate and proximate factors, and their interrelationships, thought to be important in the evolution of sociality and cooperative breeding in the Bathyergidae. Boxes outlined with bold lines indicate the principal components of the aridity food distribution hypothesis (AFDH). Modified from Bennett & Faulkes [14].

An assumption implicit in the AFDH is that increased aridity should constrain and reduce dispersal and increase within-group relatedness (R), and the limited empirical data available from appropriate intra-specific comparisons support this. Hess [21] used microsatellite genotyping to estimate relatedness in colonies of the naked mole-rat across an aridity gradient in Kenya. Although the sample size was small, a weak but statistically significant correlation was found in support of aridity constraining dispersal. Similarly, comparison of intra-colony relatedness in two populations of Damaraland mole-rats revealed a lower R value at Hotazel, South Africa, compared with a more arid site at Dordabis, Namibia [22]. Within-species comparisons of philopatry and dispersal in arid and mesic-dwelling populations of the common mole-rat (*Cryptomys hottentotus hottentotus*) 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 [23]. Furthermore, behavioural tests

on animals from the arid population revealed substantially higher levels of rejection of foreign conspecifics in dyadic encounters than the mesic population, suggesting increased xenophobia in the former [24]. These differences in dispersal indicate adaptive variation in social behaviour between the regions, and strongly suggest that delayed dispersal, sociality and cooperation may be more crucial to individual survival in arid than in mesic areas. As such, these findings provide persuasive support for the underlying contention of the AFDH, that ecological constraints on successful dispersal and/or colony formation in arid areas have promoted a greater degree of social cohesion in mole-rats occurring in these regions. Confirmation that sociality and group size are adaptive is difficult to determine empirically. However, in field studies of Damaraland mole-rats, there are significant positive effects of group size on offspring recruitment and survival (A. J. Young, N. C. Bennett and J. U. M. Jarvis 1987–1999, unpublished data), and colonies of Damaraland mole-rats with larger group sizes have a higher survival

[18]. Burda *et al.* [25] argue against a causal relationship between aridity, cooperative foraging for dispersed food resources and the evolution of sociality in mole-rats. They suggest instead that the social behaviour of mole-rats is a result of an ancestral tendency for 'cooperative monogamy' reinforced by a subterranean lifestyle that constrains dispersal (as contended by the AFDH). Clearly, at any particular point in time, an organism's phenotype is phylogenetically constrained; an ancestral mole-rat would need to either have a predisposition to family formation to facilitate cooperative behaviour, or in a changing environment selection may have favoured individuals with genotypes that enable expression of a more socially tolerant phenotype. Such a mutation would be highly adaptive in the right conditions, e.g. where ecological constraints were high, and rapidly spread through the population. Gains and losses of social phenotype appear to have occurred more than once in the Bathyergidae, and the proximate factors and mechanisms that underlie these changes will be discussed below.

5. Proximate factors

(a) Neurobiology of social behaviour

African mole-rats are extraordinary among mammals in the diversity and range of social strategies adopted by the member species, and as such, they offer a unique model system with which to address the neurobiology of sociality, together with the genetics underlying different neurobiological phenotypes. In mammals, the evolution of cooperative breeding is restricted to socially monogamous species [26], which are comparatively uncommon among mammals (5% of all mammalian species) [27]. Pair bonding, the selective and enduring attachment of a male and female, is the defining feature of monogamy. Recent studies indicate that the expression of such behaviour is dependent on particular neurobiological phenotypes, and, therefore, possession of such a phenotype is a prerequisite to pair bonding, monogamy and sociality. Key insights into the neurobiological substrates underlying the formation of monogamous and/or parent-offspring bonds have been obtained from comparative studies of voles (genus *Microtus*) that are either monogamous and social, with bi- and alloparental care, or promiscuous and solitary [28]. In this context, the neuropeptides oxytocin (OXT) and vasopressin (AVP) have been shown to be involved in modulating sociality, pair bonding and aggression [29]. Specifically, the pattern and density of receptors for OXT and AVP (the V1a receptor) differ significantly between promiscuous and monogamous voles (*Microtus* spp.) and mice (*Peromyscus* spp.) [30]. Social functions depend on whether OXT or AVP receptors are expressed at certain forebrain sites, including the nucleus accumbens and ventral pallidum; these sites incorporate dopaminergic projections from the ventral tegmental area, which signal rewards associated with cues for identifying mate, offspring, or kin [28]. Levels of both OXT receptors and OXT receptor transcript expression in the nucleus accumbens are higher in monogamous prairie voles than in promiscuous, solitary montane voles [31]. Recently, it has also been determined that the eusocial naked mole-rat exhibits higher levels of OXT receptor binding than the solitary Cape mole-rat (*Georchys capensis*) in several significant regions of the forebrain. As with social voles, OXT receptor levels in naked mole-

rats are intense and extensive in the nucleus accumbens, whereas OXT receptors are not detectable in the Cape mole-rat in this area [32]. This abundance of OXT receptor levels in the nucleus accumbens of naked mole-rats reflects their high levels of sociality, alloparenting behaviour and potential for reproductive attachments, whereas the reduced oxytocinergic signalling at this site in Cape mole-rats reflects a paucity of prosocial behaviours. Furthermore, there is a remarkable correspondence between the OXT receptor levels in some areas of the brain in the eusocial naked mole-rat and the monogamous and pair-bonding prairie vole at one end of the spectrum, and the asocial Cape mole-rat and the solitary, non-pair-bonding and promiscuous voles at the other [28,32]. Recent studies have confirmed that the Damaraland mole-rat also resembles the naked mole-rat (and social voles) with respect to OXT receptor binding being present in the nucleus accumbens. These observations suggest convergent evolution across different rodent suborders for this particular neurobiological phenotype underpinning aspects of social behaviour.

AVP has also been found to facilitate social behaviours in a number of species, including voles, and in the formation of affiliations by males AVP acting through the V1a receptor may play a more significant role than OXT, with its critical actions occurring within the ventral pallidum rather than the nucleus accumbens [28]. Comparisons between naked and Cape mole-rats have found that different distributions of V1a in several brain areas between these two species suggest an association between the vasopressinergic system and prosocial behaviours [33]. However, the patterns of receptor distribution are different to that seen in the monogamous/social and promiscuous/asocial vole model. Conversely, the high V1a receptor binding seen in the ventral pallidum of monogamous/social voles is not seen in eusocial mole-rats, but it is apparent in this region in solitary Cape mole-rats although this is not matched by presence of V1a peptide. Further, the Damaraland mole-rat unexpectedly has strong V1a receptor and peptide (AVP) binding in the nucleus accumbens, which is not seen in either social voles or naked mole-rats. Collectively, these studies suggest a combination of the retention of a particular neurological substrate (OXT receptor expression in the nucleus accumbens) and the emergence of a new one (AVP receptor expression in the nucleus accumbens) in Damaraland mole-rats, leading to the convergent evolution of social behaviour (arguing for a scenario as in figure 1*b* or *c*). Investigation of other mole-rat species will be informative in understanding the evolutionary gains and losses of these neural substrates within the family. A recent study on another social species, Ansell's mole-rat *Fukomys anselli* [34], examined the distribution of OXT and AVP immunoreactive neurons, but not receptor distributions, thus preventing a full comparison across the family. Looking beyond the Bathyergidae at other Hystricognath rodents in the family Ctenomyidae, Beery *et al.* [35] also found marked differences in OXT and V1a receptor distributions between a social and a solitary dwelling species of tuco-tuco (*Ctenomys sociabilis* and *Ctenomys haigi*, respectively). However, they exhibited a pattern of nucleus accumbens OXT and ventral pallidum V1a receptor binding that was different from that associated with the formation of opposite-sex pair bonds in voles; in particular, binding was completely absent in the nucleus accumbens. Thus, in the Ctenomyidae, it would appear that

different neural mechanisms may underpin the proximate maintenance of pair bond formation and sociality.

(b) Colony composition, cooperative behaviour and divisions of labour

At one end of the social continuum seen in African mole-rats are the asocial, strictly solitary and highly xenophobic species, where mating couples only pair up for the briefest of periods during a defined breeding season, and offspring leave the natal burrow soon after weaning [36–39]. At the opposite end of the spectrum, the eusocial species exhibit extreme reproductive skew; reproduction is confined to a single female per colony (the queen) and one to three breeding male consorts, with offspring remaining philopatric and undertaking cooperative behaviours of one form or another [2,25,40–42]. There is inter- and intraspecific variability in colony composition and reproductive and behavioural divisions of labour within the social mole-rat species (e.g. group size, skew in lifetime reproductive success and behavioural polyethism) [43,44]; hence, sociality seems to offer greater flexibility in response to the prevailing environmental constraints. The breeders constitute a clearly defined caste (i.e. a distinct group performing a specialized function) within colonies of all social mole-rats and can be discerned by their morphology and physiology [45–48]. However, extra-colony copulations and paternities may also occur to a greater or lesser extent, producing variance in lifetime reproductive success depending on the species, as discussed below [22,43,49,50].

The non-breeding colony members of both sexes may show varying patterns of task specialization and differences in the frequencies of cooperative ‘worker’ behaviour. While there are species-specific differences, there may also be variation within a species depending on colony age and size—this produces a complex relationship between body mass, age and the role of an individual within a colony. For example, in the genus *Cryptomys*, it appears that all colony members carry out such activities, performing work with a similar frequency [51,52]. These worker tasks include digging and maintaining foraging burrows, and provisioning food in both storage chambers and the nest chamber. By contrast, within the genus *Fukomys*, colonies of the eusocial Damaraland mole-rat (*Fukomys damarensis*) may have distinct groups of individuals that perform work-related tasks to differing degrees. In effect, there are smaller (but not necessarily younger) animals that perform a large proportion of the daily burrow maintenance activity and other larger (but not always older) individuals that perform little or no worker activities. This may in some colonies result in distinct groups of frequent workers, infrequent workers and non-workers [40,47]. In the Damaraland mole-rat, non-breeding workers may also carry out alloparental care such as pup grooming and retrieval of wandering pups to the nest chamber [40,47,53–55]. A similar work-related division of labour is also found in eusocial naked mole-rats which also results in a body size polyethism; all animals born enter a frequent worker group, then as they increase in body mass with age, work progressively less until they may enter a ‘non-worker’ group. Slower growing individuals may remain in the frequent worker caste, perhaps permanently, whereas faster growing animals become infrequent or non-workers or in a minority of cases, breeders. Conversely, ‘defence’-related

behaviours, such as patrolling the burrow and guarding the nest chamber, are carried out with increasing frequency as individuals increase in body size. These larger individuals are also involved in defence against conspecifics and predators (snakes) [2,56,57].

In addition to the aforementioned and sometimes striking variation in growth rates observed among some individuals within litters, plasticity in growth rates is also seen between litters, particularly in newly establishing colonies. Bennett & Navarro [58] found that Damaraland mole-rats born as first and second litters to new pairs of breeding animals grew faster, reached higher absolute growth rates and attained greater body mass than subsequent litters. This phenomenon has also been observed in the naked mole-rat; the offspring from the first two litters in a newly founded colony are the only ones where age and body mass covary for all individuals, and they also attain the greatest body mass. Growth functions also vary significantly between litters and there is an inverse trend between asymptotic body mass and litter order, with many individuals remaining small within increasing orders of litters [59,60].

In addition to correlations between body mass and worker and defence behaviours, growth, body size, and dominance and reproductive status are also linked. Dominance rank position and breeding status correlate significantly with body size in both sexes, and growth responses in non-breeders may be triggered following the death or removal of breeding animals from a colony, especially among older litter members—attainment of reproductive status is almost always accompanied by a growth spurt in the individual [60–62]. The proximate physiological cause and control of the differential growth rates observed within and among litters in both Damaraland and naked mole-rats is intriguing, and the underlying mechanism not understood. One might speculate that it could be in part due to dominance/agonistic interactions among individuals, and the physiological consequences arising from these. It is unlikely that the greater growth rates recorded in first born litters may reflect less competition for parental care in those litters when compared with later born litters, as has been shown in some communally rearing rodents. Because mole-rats have long gestational periods and inter-birth intervals (the average is 80 and 90 days between litters in naked and Damaraland mole-rats respectively), by the time a new litter arrives previous pups are no longer receiving parental care and have been recruited into the workforce. Importantly, in both eusocial mole-rat species the variation in growth and body size polyethism enables a colony to rapidly and flexibly express a spectrum of behaviours essential for survival in response to high ecological constraints. In a remarkable example of convergent evolution, there are analogies in the allocation of behavioural roles and the flexible behavioural polyethism observed within colonies of eusocial mole-rats, and social Hymenoptera such as bees. Among social insects, behavioural division of labour is also characterized by a temporal polyethism, and, at least in bees, may also show variation among hives (or colonies) in the age of onset of particular behaviours. The division of labour in the honeybee is characterized by younger workers remaining in the hive and performing tasks there, whereas older workers perform more risky outside tasks, mainly foraging. Similarly in mole-rats, smaller animals undertake less risky foraging than the more risky defence behaviours seen in larger animals. Beshers *et al.* [63] suggest a model to

explain this (that may also be appropriate to mole-rats) based on, first, an intrinsic process of behavioural development that is associated with physiological changes (with important roles played by juvenile hormone and octopamine). Second, an inhibition of development is dependent on the colony age demography, and mediated through social interactions among the workers in a honeybee colony, whereby the presence of foragers inhibits the maturation of younger bees to become foragers. This is analogous to the differential patterns of growth observed in successive litters of mole-rats.

Whether social mammals, like some social insects, also become so specialized that they form specific morphologically distinct castes is a contentious question and one that has generated much discussion, particularly in relation to what defines a eusocial species [64,65]. While the presence of fixed and distinct work-related behavioural castes is not unanimously supported in mole-rats, there is good evidence that both Damaraland and naked mole-rats have reproductively distinct castes. The first such discovery was the 'disperser morph' male phenotype in naked mole-rats, particular males that are behaviourally, hormonally and morphologically distinctive [45]. Subsequently, the morphological distinctiveness of the queen resulting from vertebral lengthening has been reported [46]. Similar adaptations have also been shown to occur in the Damaraland mole-rat, with larger infrequent workers thought to constitute a physiologically distinct dispersing caste who build up their own body reserves in preparation for dispersal and reproduction when environmental conditions are suitable (after periods of rainfall) [47]. Further, Young & Bennett [48] have recently shown a morphological divergence in body shape between breeders and non-breeding helpers, resulting from a modification of the growth trajectory of non-breeders upon the acquisition of dominant breeding status. As with the naked mole-rat, the reproductive female Damaraland mole-rat develops a distinctly longer body relative to the skull size. Intriguingly, however, the change in shape among newly dominant Damaraland mole-rat females is achieved not through a sudden body length growth spurt via vertebral elongation as reported for the naked mole-rat [46,66]. This occurs as a result of a slight decline in body length growth, coupled with a large reduction in skull width growth. Young and Bennett speculate that this socially induced plasticity in growth, and resulting morphological divergence of dominants and subordinates may reflect a reproductive status-dependent switch in resource allocation towards maximizing reproductive output rather than investing in growing the tools of the workforce (i.e. the skull and associated incisors). These subtle differences in the proximate control of social factors between naked and Damaraland mole-rats reflect the independent origin of eusociality within the Bathyergidae and exemplify the flexibility in response to similar ecological constraints.

(c) Reproduction and reproductive suppression

In the subterranean niche, the costs of finding a mate and establishing a new colony are potentially much greater than those of surface dwelling species, owing to the high energetic costs of burrowing and other ecological constraints [12]. Both solitary and social species of mole-rats need to respond appropriately and flexibly to these constraints, and, not surprisingly given their geographical range, selection has

favoured a number of physiological and behavioural adaptations. These include variation in the mode of ovulation, seasonality in breeding and, in social species, variation in reproductive skew. In some cases the latter is brought about by an extreme socially induced suppression of reproductive physiology in subordinate colony members. During the dry season or periods of prolonged drought, soils become hard and are generally not favourable for burrowing in [67]. However, the onset of rainfall softens the soil, increases food abundance and reduces the costs of mate searching in the solitary species, or dispersal and subsequent mate acquisition in social species. Thus, strong selective pressure for both seasonal reproduction and induced ovulation, where mating triggers ovulation, reducing the latency from pairing to conception, has led to the evolution of these traits in solitary species of mole-rats inhabiting regions with a predictable and seasonal rainfall (*Georchus* and *Bathyergus*) [38,40,68–70]. This is mirrored in *Cryptomys*, where induced ovulation occurs in the cooperatively breeding highveld mole-rat, *Cryptomys hottentotus pretoriae*, and the Natal mole-rat, *Cryptomys hottentotus natalensis* [71,72]. A common characteristic of these species, apart from the Natal mole-rat, is that they are all either seasonally breeding and/or dependable on regular and predictable but short lived mating opportunities. Interestingly, the Natal mole-rat appears to have retained the trait of induced ovulation while exploiting higher altitude habitats where rainfall tends to be high throughout the year.

In contrast, all species studied so far from the social genera *Fukomys* and *Heterocephalus* are spontaneous ovulators and may breed throughout the year [73–76]. In some species this appears to be in response to a reduction in seasonality at lower latitudes in habitats where rainfall is relatively high (e.g. *F. mechowii* and *F. anelli*) [20,77]. Comparative phylogenetic analysis has revealed a positive correlation between seasonality in breeding and induced ovulation. A likelihood-based reconstruction suggests that the ancestral state is induced ovulation in the Bathyergidae and that this trait has been convergently lost in at least these two lineages of cooperatively breeding mole-rats exhibiting spontaneous ovulation [75].

Eusocial naked and Damaraland mole-rats, although phylogenetically divergent, are found in similar harsh habitats where rainfall is sporadic and unpredictable, with high costs to dispersal. The resultant high degree of natal philopatry and cooperative behaviour required to exploit this niche necessitates a high reproductive skew, as predicted by theories of optimal reproductive skew [43]. There are differences in the proximate maintenance of optimal skew, dependent on the species, with key factors being inbreeding avoidance and the level of environmental constraint limiting dispersal. In the extreme, naked mole-rats are unique in that skew is maintained by a suppression of reproductive physiology, resulting in the disrupted production of mature gametes in non-breeding animals of both sexes [73,78]. This socially induced reproductive suppression is mediated by dominance and interactions with the breeding queen. It is necessary because naked mole-rats are facultative inbreeders, and have no hesitation in mating with close relatives should there be no opportunities for outbreeding—although the latter is the preferred option [79]. The Damaraland mole-rat is enigmatic in that it has both components of incest avoidance and a suppression of female reproductive physiology [80]. Because

they are strict outbreeders, incest avoidance alone could be sufficient to maintain high reproductive skew if their colonies were founded by unrelated opposite-sexed conspecifics, and contained just their offspring. However, this is not always the case, and although, like the naked mole-rat, the Damaraland mole-rat shows a high degree of natal philopatry, during periods of good rain unrelated dispersing individuals may enter functionally complete colonies. In such instances, an immigrating unrelated male could potentially mate with non-reproductive females, if the latter were not physiologically suppressed by the breeding female. Thus, by enforcing suppression on the non-reproductive females, the reproductive female ensures that plural breeding does not arise within the colony, high skew is maintained and non-breeders are available to work cooperatively [22,49,80].

In the obligate outbreeding social species of *Cryptomys* and *Fukomys* inhabiting mesic environments, where regular opportunities for dispersal and establishing independent colonies are available, the chances of establishing a new colony and to accrue reproductive success are relatively high. These mesic-adapted species have not evolved a physiological suppression, and rely solely on incest avoidance to maintain reproductive skew in colonies. Thus an immigrating unrelated male to the colony may enable the reproductive female opportunity for extra-pair copulations, but also potentially mate with subordinate females. This produces flexibility in reproductive strategy within the cooperative breeding framework, and variation in lifetime reproductive success. For example, in a study by Bishop *et al.* [50], paternity was not always assigned to the phenotypically distinguishable breeding male—both extra-colony males and subordinate males within colonies, hitherto classed as ‘non-breeders’, were also responsible for paternities. Further, there were significant differences in the proportions of these assignments to different males, depending on the habitat. At a mesic site where ecological constraints on dispersal were lower, only 19 per cent of within-colony paternities were assigned to the ‘breeding male’, with 81 per cent owing to a different within-colony male. Overall, 29 per cent of paternities were assigned to extra-colony males. Conversely, at an arid site where dispersal costs were higher, 79 per cent of within-colony paternities were assigned to the ‘breeding male’; overall, 18 per cent of paternities at the site were assigned to extra-colony males. Although suppression of reproductive physiology is not seen in this species, plural breeding among females is extremely rare, despite opportunities for mating with unrelated individuals. These disparate results are a clear exemplar of alternative reproductive strategies for males of this species, depending on the environmental conditions and the ease of movement of males between

colonies, and it is likely that similar strategies will be found in other as yet unstudied mole-rat species.

6. Conclusions

Molecular phylogenies have enabled robust comparative analyses of the Bathyergidae that can estimate gains and losses of sociality, and the interplay between the ultimate and proximate factors driving the evolution and maintenance of social behaviour and cooperative breeding. These studies show that sociality and cooperative breeding requires the correlated evolution of a mosaic of traits, including, first, the appropriate neurobiological phenotype (i.e. the ability to form social bonds), followed by a raft of behavioural (e.g. mate choice/inbreeding avoidance, division of labour) and reproductive adaptations (control of ovulation and seasonality of breeding, suppression of reproduction). Given that sociality in the context of the subterranean niche appears to be highly adaptive—social mole-rats in both *Fukomys* and *Cryptomys* successfully exploit both arid and mesic habitats—we are faced with a conundrum regarding asocial species: why do they lose the neural phenotype for social tolerance and pair bond formation when it is apparently such a successful and flexible trait allowing a range of lifestyle options? Another major challenge now is to understand the genetic basis underlying the variance in neural phenotype that facilitates long-term pair bond formation, monogamy and ultimately sociality. Previous studies have shown that the V1a receptor gene differs between monogamous and social (prairie) and promiscuous and asocial (montane) voles, and this difference has been shown to determine its expression pattern and, thus, variation in male behaviour [15,16]. Whether the differential expression of OXT and V1a receptors in asocial and social African mole-rats is determined genetically in a similar way to that seen in voles remains a fascinating question to be answered. Furthermore, does genetic variance in any way account for the different developmental pathways followed by some mole-rats, for example whether they remain a worker, or become a disperser or a breeder? A role for epigenetic effects in this context remains to be investigated. The application of newly emerging genomic data should begin to shed light on some of these issues [81].

We acknowledge research grants from the National Research Foundation, the University of Pretoria as well as a DST-NRF South African Research Chair of Mammal Behavioural Ecology and Physiology award to N.C.B. Neurobiological work was supported by BBSRC project grant no. BBD5231861 (C.G.F.).

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