

Chapter 10

African Mole-Rats: Eusociality, Relatedness and Ecological Constraints

M. Justin O’Riain(✉) and Chris G. Faulkes

Abstract Within the family of African mole-rats (Bathyergidae) there is a range of lifestyles from strictly solitary to eusocial. This variation correlates strongly with numerous ecological factors providing evidence in support of an ecological basis for the evolutionary inception and maintenance of sociality in mole-rats. Furthermore, recent studies on the relatedness of individuals both within and between neighboring colonies of social mole-rats suggest that previous arguments that expounded the importance of relatedness to the evolution of sociality were misleading. A close look at arguably the only eusocial mammal known to science, the naked mole-rat, provides a unique opportunity to study the similarities in the selective environment of insects and mammals without the associated phylogenetic noise of a close common ancestry. In addition, striking examples of convergent evolution between naked mole-rats and eusocial insects provides insight into why there are so few eusocial vertebrates.

10.1 Introduction African Mole-Rats: Ecological and Social Diversity

African mole-rats are subterranean hystricomorph rodents endemic to sub-Saharan Africa. The family is speciose with many holotypes being named in the late 19th and early 20th century. Reviewing this early literature, Ellerman (1940) listed a total of 62 species in five genera, as follows: *Heterocephalus* ($n=4$); *Heliophobius* ($n=3$); *Georychus* ($n=8$); *Bathyergus* ($n=3$); *Cryptomys* ($n=49$). Currently, the taxonomy of mole-rats is in a state of flux whilst synonymies in the nomenclature are fully investigated using modern techniques. However, recent

M. Justin O’Riain
Zoology Department, University of Cape Town, Private Bag X3, Rondebosch, 7701,
South Africa
justin.oriain@uct.ac.za

molecular phylogenetic (Faulkes et al. 2004; Ingram et al. 2004) and cytogenetic studies (Van Daele et al. 2004) support the high species diversity in *Cryptomys*, and suggest splitting this clade into two genera, *Cryptomys* and *Coetomys* (Ingram et al. 2004) or *Cryptomys* and *Fukomys* (Kock et al. 2006). In this chapter, we will adopt the traditional nomenclature of a single genus (*Cryptomys*). Figure 10.1 presents a simplified phylogeny showing the relationships between genera, their estimated divergence times and social structure.

Mole-rats in the genera *Heliophobius*, *Bathyergus* and *Georchus* all adopt a strictly solitary lifestyle and are generally restricted to regions of higher precipitation (greater than 400 mm per annum). Of these, *Heliophobius* has the widest distributional range and occurs in the sandy soils of savannas and woodlands of southern Kenya, throughout Tanzania and parts of southeastern Zaire, through Malawi to central Mozambique. The other two solitary genera are much more restricted in their ranges. *Bathyergus* is endemic to some coastal areas of South Africa and southern Namibia, and *Georchus* occurs in several disjunct populations within South Africa. In the two remaining genera (*Cryptomys* and *Heterocephalus*) all taxa investigated so far exhibit social behavior, and are found in both mesic and xeric regions. *Heterocephalus* occurs in the arid regions of East Africa (parts of Kenya, Ethiopia and Somalia). The areas they inhabit are characterized by low (less than 400 mm per annum) and unpredictable rainfall, with on average only 4 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; Jarvis et al. 1994). The *Cryptomys* genus is the most widely distributed of all the extant bathyergids, ranging throughout South Africa, and extending into part of Mozambique and Zimbabwe, and southern, central and western Africa. They are apparently absent from the horn of Africa, tropical rainforests of central and west Africa, and the Sahara. As with *Heterocephalus*, the ranges of some of these social Cryptomids extend into areas of very low, sporadic and unpredictable rainfall (sometimes <200 mm per annum). However, some species also occur in mesic areas, like the common mole-rat, *Cryptomys hottentotus hottentotus*. The relationship between sociality and habitat aridity will be discussed in more detail below.

Molecular phylogenies of the Bathyergidae are firmly rooted in East Africa, with *Heterocephalus* and *Heliophobius* forming the basal lineages (Fig. 10.1), and the common ancestor of the family dated to approximately 40–48 million years ago (Huchon and Douzery 2001). The subsequent adaptive radiation and spread of the family across sub-Saharan Africa appears to have been influenced by Rift Valley formation and its affect on geomorphology, vegetation and climate (Faulkes et al. 2004; Faulkes and Bennett 2007) and the changing patterns of drainage of major river systems (Van Daele et al. 2004; Van Daele et al., 2007). The variation in patterns of social behaviour across the family has presumably been a response to these environmental challenges, and has led to the convergent gains and/or losses of sociality that we will elaborate on below (Fig. 10.1).