Eusocijalnost u Afričkih sljepaša

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EUSOCIALITY IN AFRICAN MOLE-RATS
EUSOCIJALNOST U AFRIČKIH SLJEPAŠA

SEMINAR PAPER

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CONTENTS

1. INTRODUCTION

The African mole-rats, family Bathyergidae, are strictly subterranean hystricomorphic rodents endemic to sub-Saharan Africa. Ellerman (1940) listed a total of 62 species in five genera: *Heterocephalus, Heliophobius, Georychus, Bathyergus, Cryptomys.* African mole-rats have been known to scientists for more than 220 years (*Georychus capensis* being described by Pallas in 1778), with the last genus, *Heliophobius*, discovered more than 150 years ago by Peters in 1846, and many new species and subspecies named in the late 1800s and early 1900s (Burda et al. 2000). According to O'Riain and Faulkes (2008) their taxonomy is still in a state of flux and needs to be reviewed. However, a recent review of biodiversity in Bathyergidae family suggests 30 or more species in six genera (shown in figure 1): *Heterocephalus*, *Heliophobius*, *Georychus*, *Bathyergus*, *Cryptomys*, *Fukomys* (Faulkes and Bennet 2013).

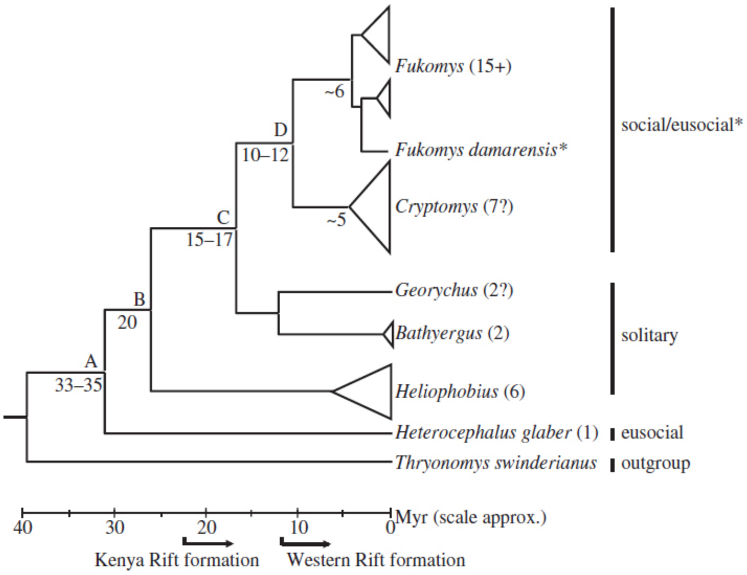

Figure 1. Simplified phylogeny for the Bathyergidae, including the closest outgroup; the cane rat (*Thryonomys swinderianus*). Taken from Faulkes and Bennett (2013).

This taxon is unique in that it exhibits the widest range of social systems of any mammal. These range from solitary (*Heliophobius*, *Bathyergus*, and *Georychus*), to social (*Cryptomys* and *Fukomys*), and eusocial Damaraland mole-rat (*Fukomys damarensis* Ogilby, 1838) and Naked mole-rat (*Heterocephalus glaber* Rüppell, 1842). The two last mentioned species are highly social and characterized by overlapping generations, reproductive division of labour within their colonies, and cooperative care of offspring (Jarvis 1981, Jarvis and Bennett 1991). Those characteristics were defined by Wilson (1971) as the criteria for eusociality. In fact, one of the most frequently emphasized attributes of mole-rat biology has been their “eusocial” system, and eusociality in mammals has long been equated with the social system seen in the naked mole-rat and Damarland mole-rat (Burda et al. 2000).

2. EUSOCIALITY

The term “eusocial” (truly social) was first used by Batra (1966) to describe nesting behaviour in bees in which the nest-founding parent survives to cooperate with a group of her mature daughters, with division of labour. Michener (1969) formalized the classification of bee social systems and comprised three qualities: (1) castes and division of labour; (2) generation overlap between mother and their adult offspring; (3) and cooperative work on cells. Wilson extended Michener's terminology to other social insects, and composed the definition of eusociality commonly used today: (1) individuals of the same species cooperate in caring for the young; (2) there is a reproductive division of labour, with more or less sterile individuals working on behalf of fecund nest mates; (3) and there is an overlap of at least two generations in life stages capable of contributing to colony labour, such that offspring assist parents during some period in their life (Crespi and Yanega 1995).

One particular problem with Wilson’s definition of eusociality was that the phrase “reproductive division of labour” has no clear meaning. Its vagueness has allowed for various different interpretations resulting in different taxa being classified as eusocial by divergent, often unspecified, criteria. Crespi and Yanega (1995) thus proposed redefining of the term “eusociality” and they argue for the restriction of eusociality to species characterized by permanent morphological castes (groups of individuals that become irreversibly behaviourally distinct at some point prior to reproductive maturity). Oppositely, Sherman et al. (1995) adopted a more expanded view and attempts to classify all species with evidence of reproductive skew as eusocial. Sherman et al. (1995) also argued that evolutionary explanations for sociality in vertebrates and invertebrates will be best understood if common selective factors are identified rather than independent explanations sought for each taxonomic group (O’Riain and Faulkes 2008).

Burda et al. (2000) defined eusociality in mammals by reproductive altruism (which involves reproductive division of labour and cooperative alloparental brood care), overlap of adult generations, and permanent philopatry. They argued that additional criteria such as the existence of castes, colony size, reproductive skew, and social cohesion are not pertinent to the definition of eusociality in mammals.

These are just some examples of different approaches and definitions various authors provided for the concept of eusociality in mammals and other animals, and the following chapters will review eusociality and evolution of sociality in the Bathyergidae.

3. SOCIAL EVOLUTION IN AFRICAN MOLE-RATS

African mole-rats are found from the Cape region of South Africa through to disjunctive populations in Southern Sudan in the north, Somalia in the east and Ghana in West Africa. They inhabit a variety of soil types in different biomes and climatic zones, and 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. African mole-rats feed exclusively on underground roots and tubers (geophytes) which means they are not found in heavily forested regions or in extreme deserts. It appears that solitary mole-rats are mainly restricted to moderately moist (mesic) regions of higher rainfall while the social genera are found in both mesic and xeric (dry) regions, with the *Heterocephalus* genus appearing exclusively in the xeric regions of East Africa (Faulkes and Bennet 2013).

Having in mind the wide range of African mole-rats, as well as the variety of climates they inhabit, it is logical to assume that there exists a connection between distribution of species with different social phenotypes and ecological constraints of their habitats. Figure 1 shows factors, and their interrelationships, thought to be important in the evolution of sociality in the Bathyergidae.

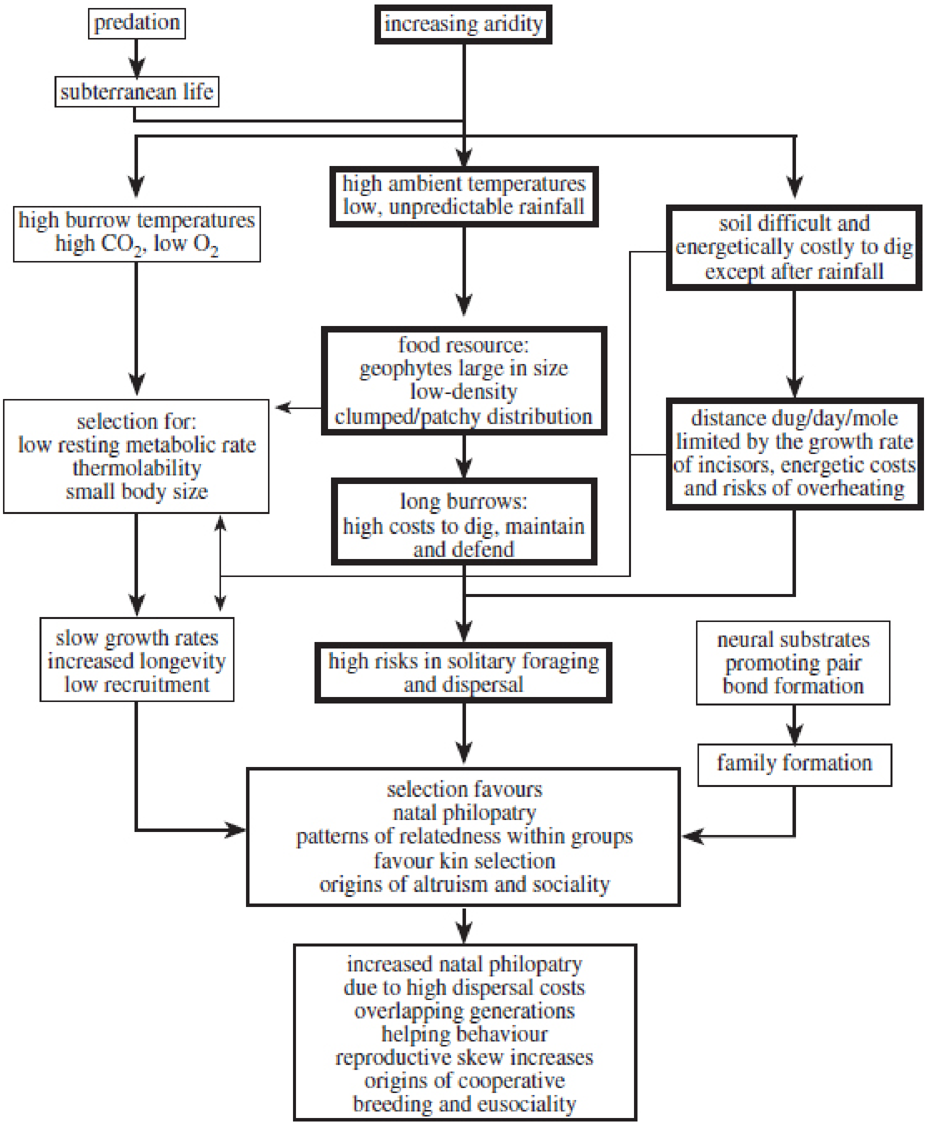

Figure 2. Taken from Faulkes and Bennet (2013).

3.1. Aridity-Food-Distribution Hypothesis

A number of authors have argued that the distribution, size, and digestibility of the geophytes upon which mole-rats feed, as well as the variation and predictability of rainfall have played an important role in the evolution of sociality in the Bathyergidae. This has become known as AFDH: Aridity-Food-Distribution Hypothesis (O'Riain and Faulkes 2008).

While predation and predator avoidance might be a major drive for evolution in some animals, it is not considered that these play a major role for social evolution in the Bathyergidae family. Their main predators (mole snakes and birds of prey) are prevalent across all mole-rat habitats and yet level of sociality differs (Faulkes and Bennet 2013).

Faulkes and Bennet (2013) argue that costs and constraints (e.g. dispersal and new burrow formation may be costly as digging through soil is energetically expensive) associated to underground living are the ultimate drivers in social evolution of mole-rats. Along with constraints of underground living, AFDH takes into consideration the distributions of roots and tubers mole-rats consume. In mesic regions these foods would be more uniformly distributed, whereas in xeric regions the plants would be more widely dispersed or occur in patchily distributed high-density clumps.

The AFDH brings together these environmental constraints as an explanation for social evolution in the Bathergidae. 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 (Faulkes and Bennet 2013). From this explanation, we can see that AFDH also explains why social and eusocial mole-rat genera occur in xeric regions while solitary genera prefer mesic regions.

Burde et al. (2000) argue that AFDH is not sufficient to explain social evolution in mole-rats, and instead they suggest that social behaviour of mole-rats is a result of a social common ancestor of the family. Even though eusociality may be the ancestral state of all mole-rats, such approach doesn’t explain why there exists such a variety of social systems in current mole-rat species. Whereas the AFDH tells us that the degree of sociality is affected by, amongst other factors, the quality of the habitat.

Following on from this, it is clear that with social mole-rats, sexually mature adults that retain their offspring would benefit from increased survival of their offspring in addition to increased personal survival. Parents that evict their offspring would have less success at procuring sufficient food and so would their offspring. It is therefore argued that evolution of sociality was sparked by retention of offspring in the natal territory with factors such as costs of underground living and food dispersal being promoters of sociality as a successful lifestyle. Deriving criteria of eusociality thereafter is relatively simple: (1) parents maintain a monopoly on reproduction because of incest avoidance; (2) there is an overlap of generations because of the high costs and risks associated with offspring dispersal; and (3) independent foraging and cooperative care of the young born to the colony is expected because helping to raise related young is the best way for offspring to increase their inclusive fitness (O'Riain and Faulkes 2008).

3.2. Colony Size

Colony size is generally associated with the degree of sociality, but it hasn't been directly connected with the AFDH. It is apparent that, in habitats with high costs of dispersals, offspring will benefit from staying at home until ecological conditions improve. It follows logically that conditions that allow for reproduction but limit dispersal will result in larger colony size provided all other variables are fairly constant. Another important variable influencing colony size is the longevity of breeders; the longer the lifespan of breeders, the larger the size of the colony. This is especially noticeable in naked mole-rat colonies with breeding females capable of sustained reproduction for 27 years. Naked mole-rats are known for their extremely large group sizes (up to 300 individuals) attributed to combination of long-lived breeders capable of producing large numbers of offspring for a prolonged period of time, low dispersal rates, and facultative inbreeding. By contrast, dispersal rates in other social mole-rats are high, breeder survival is low and most species studied to date are obligate outbreeders resulting in much smaller colonies (O'Riain and Faulkes 2008).

Habitat, food dispersal, and underground living costs may be the ultimate drivers for social evolution in mole-rats, but it appears the social phenotype has occurred and disappeared more than once during the evolution of mole-rats. Faulkes and Bennet (2013) show that sociality and cooperative breeding require the correlated evolution of a number of proximate factors and mechanisms; neurobiology of social behaviour (i.e. the ability to form social bonds), colony composition, cooperative behaviour (e.g. mate choice/inbreeding avoidance), divisions of labour, and reproduction and reproductive suppression.

4. EUSOCIAL MOLE-RATS

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. 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 (Faulkes and Bennet 2013).

This “extremely social” end of the spectrum is the focus of the following chapters where I will review the meaning of eusociality in two mole-rat species that are still widely accepted as the only eusocial mammals; naked mole-rat and Damaraland mole-rat.

4.1. Naked mole-rats

The Naked mole-rat (*Heterocephalus glaber*) inhabits the arid regions of East Africa, including Kenya, Ethiopia and Somalia. It lives entirely underground in colonies which often contain 70-90, but sometimes up to 300 individuals. Their burrow systems contain communal nest and toilet chambers and an extensive network of foraging tunnels, which lay total 2-3 km in length (Jarvis 1981, 1985). A characteristic and unique feature of naked mole-rat colonies is the extreme behavioural and reproductive division of labour where smaller individuals act as workers while larger individual may have defensive roles (soldiers). Reproduction is restricted to a single breeding female and one to three males. Colonies generally consist of nuclear families, so workers gain inclusive fitness benefits by assisting in the production of offspring by the queen (Ciszek 1999). This division is seen in both captive and wild colonies (Jarvis 1981). The remaining colony members do not breed and are reproductively supressed, but not sterile; ovulation in females is blocked whereas non-breeding males are still capable of spermatogenesis (Faulkes and Abott 1991).

Having in mind the above mentioned information, it is easy to understand why for over a decade, naked mole-rats were regarded as the world's only eusocial mammal. However, neither colony size nor the presences of castes are prerequisites of the original definitions of eusociality composed by Wilson (1971). Regardless, O'Riain et al. (2000) presented convincing data that female naked mole-rats do undergo a physical transformation following the attainment of reproductive status (similar to physogastry in eusocial termites). This proved that complete dimorphism exists within colonies and that these physical differences equate to irreversible morphological caste in eusocial termites. The finding that a mammal has evolved morphologically discrete queen/worker castes is the most convincing evidence to date of convergent evolution in the lifestyle of an insect and mammal. Characteristics shared by

Naked mole-rats and termites are facultative inbreeding, specialized dispersals morphs for occasional outbreeding during optimal ecological conditions, long lived “queens” that are exempt from dispersal once established within their colonies thanks to inbreeding. They do not have to engage in either costly or risky behaviours and are free to focus their energies on reproduction, producing large colonies exempt from dispersal once established within their colonies due to facultative inbreeding (O’Riain and Faulkes 2008). While Naked mole-rats are in many aspects similar to eusocial insects, they differ in that they do not have a clearly defined reproductive male, but other similarities are numerous (Jarvis, 1981).

4.1.1. Inbreeding

Inbreeding was long considered to be an important selective factor in the evolution of eusociality in naked mole-rats. However, a study conducted by Hess (2004) suggested that relatedness within and between their colonies was greatly overestimated because they failed to take into account environmental and historical influences. Hess’s study reported relatedness values that were not significantly different than 0.5 level expected for siblings of randomly mated parents. And average levels of relatedness are thus similar to the obligatory outbreeding Damaraland mole-rat whereas occasional high levels of relatedness are a consequence of limited dispersal opportunities (O’Riain and Faulkes 2008)

Furthermore, O’Riain et al. (1996) conducted a study of 48 captive naked mole-rat colonies and reported a discovery of a dispersal phenotype that may occasionally promote outbreeding. Dispersers are morphologically and behaviourally different than non-dispersers in that they have a greater total body fat (which may serve as a nutritional safeguard) as shown in Figure 2, a strong urge to disperse, elevated levels of luteinizing hormone, and only mate with non-colony members. This evidence shows that new colonies of naked mole-rats are sometimes founded by unrelated dispersers.

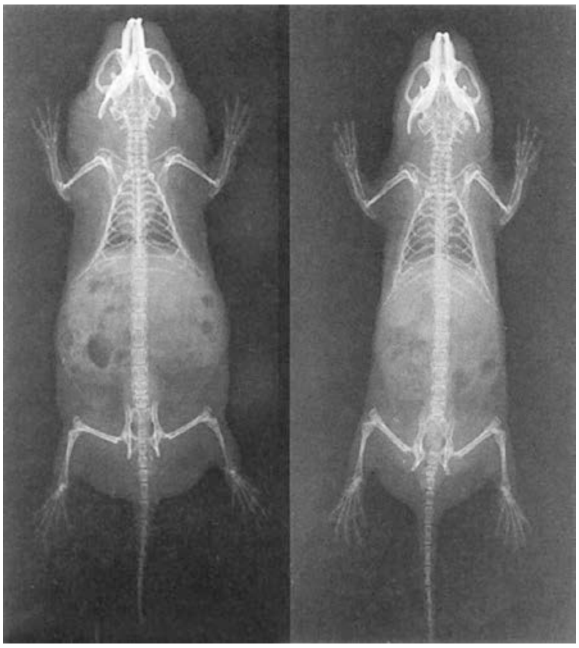

Figure 3. X-ray images of a disperser (left) and a non-disperser (right). Taken from O'Riain et al. (1996).

4.1.2. Reproductive suppression

As it was already mentioned, non-breeding members of the colony are reproductively supressed by the queen. However, this suppression can be reversed following the death or removal of the queen. So far, studies have shown that the queen is the most aggressive colony member and that reproductive suppression is achieved mainly by behavioural interactions between the queen and other colony members where the stress by social contact inhibits reproductive physiology. A primer pheromone in her urine is thought not to play a critical role in reproductive suppression (Clarke and Faulkes, 1997).

Aggression in the form of shoving (prolonged pushes involving nose to nose contact) is frequently observed in captive naked mole-rat colonies and is initiated by breeders. The queen uses shoving as a mean to incite reproductive suppression amongst other colony members. It was also thought that shoving may stimulate work activity amongst non-breeding colony members, however, these two predictions were tested in captive colonies and results showed that shoving was strongly associated with reproductive status, whereas no evidence for work activity stimulation was found (Clarke and Faulkes, 1999).

The queen (and to a lesser extent breeding males) is mostly aggressive towards larger and older colony members, mainly other females, that pose a threat to her status. In an experiment conducted by Clarke and Faulkes (1999) nonbreeding females on becoming reproductively active directed most shoves and bites at other high-ranking individuals showing signs of reproductive activity, until their reproductive dominance was established.

In males, clear hormonal differences have been found between breeding and non-breeding males. Most non-breeding males produce fewer and non-motile spermatozoa than breeding males which suggests that suppression of reproductive hormones may correlate with reduced fertility. However, within non-breeding male there is a number of individuals that are reproductively active and potentially fertile, should the breeding queen solicit them for mating (Faulkes et al. 1994).

4.2. Damarland mole-rats

Damaraland mole-rats live in the arid grasslands of southern Africa in underground colonies, much smaller in size than those of naked mole-rats. Their groups consist of two to forty individuals with one breeding female that acts as the queen and monopolizes reproduction. The remaining non-breeding members appear to be divided into frequent and infrequent workers (Bennet and Navarro, 1996). For most of the year the dry sand substrate in which Damaraland mole-rats make their burrows is too costly to dig through and that makes it an ecological constraint that works in favour of philopatry. However, periods of sustained rainfall stimulate excavation of workers of both sexes in search of food, mating and dispersal opportunities. Studies have shown that female Damarland mole-rats disperse alone to found new colonies while males usually disperse alone or in pairs, later either joining the females or dispersing into already existing colonies (Young et al. 2015)

Unlike Naked mole-rats, Damarland mole-rats are obligatory outbreeders, thus ruling out high levels of relatedness as the main factor for evolution of eusociality. Burland et al. (2002) conducted a study using captive colonies of Damarland mole-rats and their results show low levels of relatedness among breeding pairs which was to be expected. However, results also showed that relatedness is higher among females than males. From that it can be concluded that dispersal into existing colonies is male based (Burland et al. 2002). It appears then that, similar to naked mole-rats, eusociality in Damaraland mole-rats also arose as a result of the offspring of unrelated parents remaining in the natal colony.

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6. SUMMARY

Researchers have come a long way in understanding the social evolution in African mole-rats since they were first discovered more than 220 years ago, and today we know there is a connection between habitats and variations of social systems within the Bathyergidae family; solitary types occur in mesic regions with uniformly distributed food whereas social types occur in xeric regions. Social mole-rats, with the exception of the naked mole-rat, are obligatory outbreeders, and on the example of the Damarland mole-rat, we can see that given the right ecological conditions, non-breeding colony members will disperse. In the case of naked mole-rats, their eusociality was long contributed to high relatedness values within their colonies, however recent studies wielded results that go against that theory. Some studies attributed evolution of sociality to ancestral social systems, but they didn't offer an explanation for the diversity of social systems in present Bathyergidae. One of the theories that explains why some mole-rats are social and some are not is Aridity-Food-Dispersal hypothesis, but there are many other factors to be taken into consideration. And finally, progress was also achieved in researching the evolution of eusociality in the naked mole-rat and Damaraland mole-rat. However, the question arises whether we can describe any mammal as eusocial without first revising the definition of eusociality itself, seeing as a universal explanation for evolution of sociality in both vertebrates and invertebrates does not currently exists, and this is possibly something that could be the focus of future studies.

7. SAŽETAK

Znanstvenici su prošli dugi put u razumijevanju razvoja socijalnosti u Afričkih sljepaša od kada su prvi puta otkriveni prije više od 220 godina. Danas znamo da postoji veza između staništa i razvoja socijalnosti unutar Bathyergidae; solitarne vrste se javljaju u umjereno vlažnim staništima, dok se društvene vrste javljaju u suhim staništima. Društveni sljepaši se obligatorno pare sa jedinkama sa kojima nisu u bliskom srodstvu, sa iznimkom golokrtičastog štakora, te se na primjeru Damaralandskog sljepaša može uočiti da tokom povoljnih ekoloških prilika ne-reproduktivne jedinke napuštaju koloniju. Razvoj eusocijalnosti je u slučaju golokrtičastih štakora, dugi niz godina pripisivan visokom stupnju srodstva unutar kolonije, no daljnja istraživanja su pokazala da to ipak nije slučaj. Neka istraživanja pripisuju razvoj eusocijalnost pretku Afričkih sljepaša za kojega se smatra da je živio u kolonijama, no ne navodi se objašnjenje za veliku raznolikost današnjih socijalnih sustava unutar porodice. Jedna od teorija koja objašnjava zašto su neki Afrički sljepaši solitarni, a drugi žive u kolonijama je “Aridity-Food-Dispersal” hipoteza, ali postoji mnogo drugih faktora koje treba uzeti u obzir. Napredak je također uočljiv i u istraživanju evolucije eusocijalnosti u golokrtičastog štakora i Damaralandskog sljepaša. No tu se javlja pitanje da li se bilo koji sisavac može nazivati eusocijalnim bez da se prije promijeni definicija eusocijalnosti kao takve jer općenito objašnjenje evolucije eusocijalnosti u kralješnjaka i beskralješnjaka trenutačno ne postoji, te je to tema na koju bi se mogla usredotočiti buduća istraživanja.