

Seasonality of reproduction in Bathyergidae is a function of group size: A novel hypothesis (Rodentia)

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Abstract. In the African mole-rat family (Bathyergidae), species show both year-round and seasonal breeding patterns even though all species inhabit regions with varying seasonal rainfall patterns (a well-known selection driver of seasonal breeding). This short review suggests a novel hypothesis explaining why some African mole-rat species breed seasonally and others year-round. Namely, group-living African mole-rat species (with a mean colony size greater than five) exhibit an aseasonal reproduction pattern, as breeders, particularly females, possess year-round high body conditions. This is likely due to access to abundant and high-quality resources (food and water) throughout the year and reduced frequency of engaging in strenuous activities, such as digging, due to the increased efficiency of locating and retrieval of resource as a function of group size. While in the solitary and social species, with mean colony sizes of five or less, there are too few colony members to provide sufficient cooperative care benefits, the breeders show a seasonality to their body condition and thus breeding investment. As such, we hope to start a discussion on how group size could affect circannual breeding rhythms and propose some avenues for future research.

Key words. African mole-rats, reproduction, seasonality, sociality, group size, breeding.

REPRODUCTION IN SMALL MAMMALS

A positive energy balance (energy acquired from resources (food and water) / daily energy expenditure) is essential for all mammals to survive and thrive in any habitat. Furthermore, mammals that possess a positive energy balance (good access to resources and/or low daily energy expenditure) often have a good body condition resulting from the surplus of available energy being diverted to non-essential critical survival processes, such as the immune system and reproduction (CLAUSS et al. 2021).

Reproduction in mammals, especially small mammals, requires a significant investment of energy and resources and, therefore, a good body condition and a positive energy balance. Furthermore, a successful reproductive event requires a positive energy balance to allow for the optimal body condition for the breeding animal, mainly the female, and the maximal growth rates and survival of the offspring. The availability of resources, namely food and water, often controls when and the frequency at which a small mammal reproduces (CLAUSS et al. 2021). Consequently, annual rainfall patterns, and subsequent food availability have been highlighted

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Table 1. Seasonality Index (SI), derived by WALSH & LAWLER (1981). Triangles indicate seasonality of rainfall

| SI | precipitation regime | rainfall pattern | symbol |
|-----------|---|---------------------|--------|
| 0.19 | precipitation spread throughout the year | rainfall year-round | ▼▼▼▼▼ |
| 0.20–0.39 | precipitation spread throughout the year, but with a definite wetter season | rainfall year-round | ▼▼▼▼▼ |
| 0.40–0.59 | rather seasonal with a short dry season | seasonal rainfall | ▼▼▼▼ |
| 0.60–0.79 | seasonal | seasonal rainfall | ▼▼▼ |
| 0.80–0.99 | marked seasonal with a long dry season | seasonal rainfall | ▼▼ |
| 1.00–1.19 | most precipitation in <3 months | seasonal rainfall | ▼ |

as one of the strongest evolutionary drivers of when and how often a small mammal reproduces (CLAUSS et al. 2021). This is because rainfall increases not only the abundance of food but the quality. Furthermore, small mammals often use less energy in foraging during periods of increased rainfall as food is more easily found, which leaves an energy surplus that can be invested into reproduction.

Annual rainfall patterns vary across the planet, with some regions experiencing consistent rainfall throughout the year (Seasonality index, SI: 0–0.39, see Table 1), while other regions experience annual fluctuations (known as seasonality) in their rainfall (SI: 0.4–1.2, see Table 1; WALSH & LAWLER 1981). In regions with consistent rainfall throughout much of the year, reproduction often mirrors this pattern, and small mammals have the potential to breed throughout the year (an aseasonality of breeding), whereas those inhabiting regions with defined periods of increased rainfall show a distinct seasonality to their reproduction (seasonality of breeding; FITZGERALD & McMANUS 2000, IMS 1990). As such, seasonal breeding in small mammal reproduction is often confined to specific periods of the year, which ensures optimal body condition for the breeding female and the maximal growth rates and survival of the offspring (wet season) (FITZGERALD & McMANUS 2000, IMS 1990). Conversely, when conditions become unfavourable (dry season), many small mammal species cease all reproductive activity and channel their time and energy into more vital and immediate processes, such as foraging, to survive (BELHOCINE et al. 2007, ALAGAILI et al. 2017, HART et al. 2018, 2020a, 2021a, KHOKHLOVA et al. 2000). Furthermore, seasonally breeding small mammals often use consistent and predictable environmental parameters, such as photoperiod, temperature and humidity, to name a few, as proxies of when rainfall should occur (BRONSON & HEIDEMAN 1994, MEDGER et al. 2012, ALAGAILI et al. 2017, HART et al. 2018, 2020a, 2021a). These *zeitgebers* of the circannual breeding rhythm are decisive controlling factors of seasonal breeding even under laboratory conditions (KARSCH et al. 1989). However, a third common breeding strategy in small mammals is opportunistic breeding. These species breed throughout the year and only cease breeding if conditions are too harsh for reproduction and the survival of their offspring, with food availability appearing to be the primary cue to determine if reproduction occurs in these opportunistic breeders (BRONSON 1985).

All three strategies lead one to conclude that investment into reproduction depends on the female’s body condition, which is ultimately controlled by access to an abundance of high-quality food linked to rainfall.

AFRICAN MOLE-RATS

African mole-rats (Bathyergidae) are a family of small subterranean mammals (rodents) from sub-Saharan Africa, often occurring in large underground burrow systems (BENNETT & FAULKES 2000). The underground tunnel systems provide a relatively thermo-stable environment (BENNETT et al. 1988, ROPER et al. 2001, ŠUMBERA et al. 2004, BURDA et al. 2007, HOLTZE et al. 2018, ŠUMBERA 2019, HART et al. 2021b) with limited access to light. They also occur in various climates, elevations and substrates with behavioural and physiological adaptations corresponding to these conditions (FAULKES et al. 2004, HART et al. 2022a, MCGOWAN et al. 2020, ŠUMBERA 2019, VISSER et al. 2019, WALLACE et al. 2021). All species of African mole-rat studied to date inhabit regions that experience a seasonal rainfall pattern (although rainfall in some arid regions may sometimes fail or occur sporadically during the projected wet period; Fig. 1).

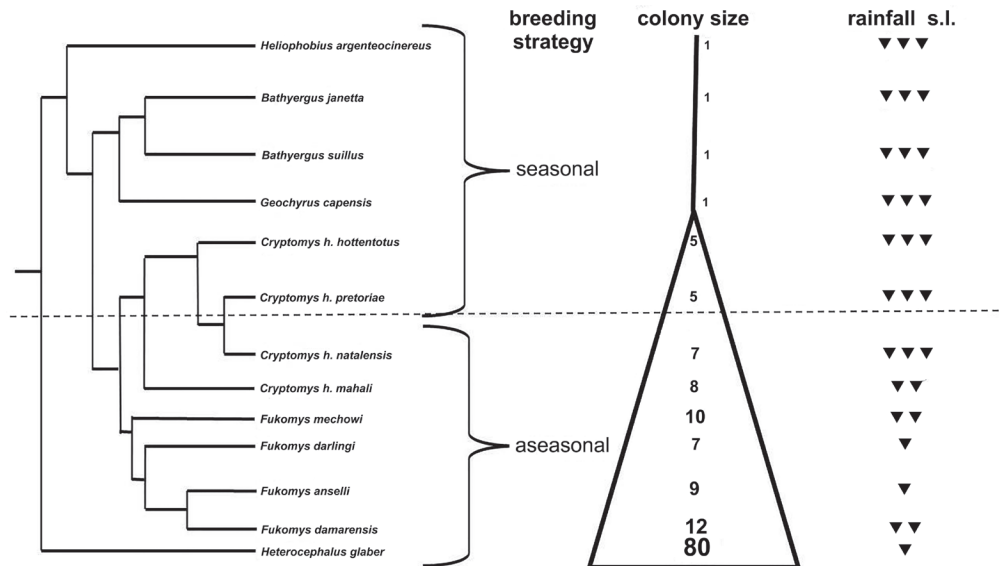


Fig. 1. A phylogenetic tree (adapted from VISSER et al. 2019) showing the evolutionary relationships of species of African mole-rats representing all six genera. Life-history information, namely breeding strategy (seasonal or year-round –aseasonal breeding) and mean colony size (solitary species are denoted with a mean colony size of 1), have been included for each African mole-rat species. The rainfall seasonality index (S.I.) is provided for each species (see Table 1 for details). Reproductive strategy, colony size and locality information from relevant studies (see Table 2). These studies are from single localities and may not represent the breeding strategies of the whole species across its distribution. Rainfall S.I. was calculated using the methods set out by WALSH & LAWLER (1981), and monthly rainfall (from 1981 and 2020) data were gathered using the methods outlined by HART et al. (2022). Monthly rainfall data were sourced for each species (using published papers regarding each species’ reproductive strategy – see Table 2) from ERA5-Land of the European Centre for Medium-Range Weather Forecasts-the latest generation created by the Copernicus Climate Change Service (MUÑOZ-SABATER et al. 2021).

Table 2. Details regarding the 13 species of African mole-rat, including reference literature, used in this hypothesis. Colony size range and capture zones, with relevant approximate yearly rainfall and habitat type (aridity index), were provided for each species. Habitat type (aridity index) was calculated and characterised as described by JACOBS et al. (2022). Abbreviations: csr – colony size range; ayr – approximate yearly rainfall [mm]; countries: TZ – Tanzania, SA – South Africa, WC – Western Cape, NC – Northern Cape, ZM – Zambia, ZW – Zimbabwe, NA – Namibia, KY – Kenya

| species | csr | location (coordinates) | ayr | habitat type | reference |
|--------------------------------------|-------|--|-------|---------------|----------------------------------|
| <i>Heliophobius argenteocinereus</i> | 1 | Mvomero District TZ (−6.82, 37.67) | 2,000 | hyper-humid | NGALAMENO et al. (2017) |
| <i>Bathyergus janetta</i> | 1 | Kamieskroon SA (−30.21; 17.92) | 250 | arid | HERBST et al. (2004) |
| <i>Bathyergus suillus</i> | 1 | Cape Town SA (−33.58; 18.37) | 500 | dry sub-humid | HART et al. (2006a) |
| <i>Georchus capensis</i> | 1 | Cape Town SA (−33.58; 18.37) | 500 | dry sub-humid | BENNETT & JARVIS (1988a) |
| <i>Cryptomys h. hottentotus</i> | 2–14 | Sir Lowry’s Pass, WC SA (−34.80; 18.85) | 650 | humid | SPINKS et al. (1999b, 2000) |
| | | Steinkopf, NC SA (−29.82; 16.85) | 145 | arid | |
| <i>Cryptomys h. pretoriae</i> | 2–12 | Gauteng SA (−26.06; 27.46) | 680 | dry sub-humid | JANSE VAN RENSBURG et al. (2002) |
| <i>Cryptomys h. natalensis</i> | 2–16 | KwaZulu Natal SA (−29.19; 29.43) | 1570 | hyper-humid | OOSTHUIZEN et al. (2008) |
| <i>Cryptomys h. mahali</i> | 2–20 | Gauteng SA (−25.39; 28.02) | 535 | semi-arid | HART et al. (2021b) |
| <i>Fukomys mechowii</i> | 2–15 | Copper Belt ZM (−10.40; 20.85) | 1130 | hyper-humid | SICHILIMA et al. (2008) |
| <i>Fukomys darlingi</i> | 2–9 | Goromonzi ZW (−17.85; 31.37) | 700 | hyper-humid | BENNETT et al. (1994) |
| <i>Fukomys anelli</i> | 2–16 | Lusaka ZM (−14.65; 27.48) | 970 | hyper-humid | SICHILIMA et al. (2011) |
| <i>Fukomys damarensis</i> | 2–41 | Dordabis NA (−22.94; 17.66) | 300 | arid | BENNETT & JARVIS (1988b) |
| <i>Heterocephalus glaber</i> | 2–250 | Mtito Andei KY (2.69; 38.16) | 300 | arid | JARVIS (1991) |

The social organisation in African mole-rats ranges from strictly solitary species through to social (colony size range of 2–20 in social species) and all the way to eusocial or truly social (colony size range of 2–300 in eusocial species) (Fig. 1; BENNETT & FAULKES 2000). African mole-rats obtain their nutrient and water requirements from the storage organs of underground geophytes (BENNETT & JARVIS 1995, SPINKS et al. 1999a, MALHERBE et al. 2003). The distribution of these geophytes and the predictability and abundance of rainfall play a crucial role in shaping sociality within the family of Bathyergidae (JARVIS et al. 1994, FAULKES & BENNETT

2013). The importance of these ecological factors has given rise to the ‘Aridity, food distribution hypothesis’ as posited by JARVIS et al. (1994) and, more recently, the ‘Behavioural osmoregulation hypothesis’ coined by HART et al. (2022a). Both JARVIS et al. (1994) and HART et al. (2022a) suggest that the evolution of social living may negate several environmental pressures, including seasonal scarceness and access to food and water. For example, in species that form large groups (see Fig. 1, Table 2), animals can increase water turnover as water and food are not limited resources as the increased group size allows for the efficient locating and retrieval of food and indirectly water (behavioural osmoregulation) (HART et al. 2022a). However, an alternative hypothesis has been proposed that African mole-rats may have been initially social, and this could represent the ancestral state; however, this social condition has been suggested to have been subsequently lost in solitary species (BURDA et al. 2000).

Social and eusocial African mole-rat species exhibit a reproductive division of labour where reproduction is often monopolised by a single breeding female and male within the colony (BENNETT & FAULKES 2000). The remaining colony members (non-breeders) are reproductively quiescent while in the colony (BENNETT et al. 1993, 1997, 1999, 2018, BURDA 1995, OOSTHUIZEN et al. 2008, MEDGER et al. 2019, SPINKS et al. 1999b, CLARKE et al. 2001, HART et al. 2022b, c). Non-breeders often perform cooperative behaviours, including pup rearing, colony defence, foraging, tunnel maintenance and burrow extension (JARVIS 1981, THORLEY et al. 2018, BENNETT & FAULKES 2000, SIEGMANN et al. 2021). A marked division of labour with breeders spending less time being active, including spending less time digging and foraging, than their non-breeding counterparts, has been observed in most, but not all African mole-rats species (SCANTLEBURY et al. 2006, LACEY & SHERMAN 2009, OOSTHUIZEN & BENNETT 2015, FRANCIOLI et al. 2020, HOUSLAY et al. 2020, JACOB et al. 2021, 2022, FINN et al. 2022).

Breeding colony members often show increased body condition compared to non-breeders; this pattern is particularly evident in arid dwelling species (SCANTLEBURY et al. 2006, HOUSLAY et al. 2020, HART, BENNETT & SCANTLEBURY unpubl. data). It is believed the dispositional state of body condition is driven by the marked division of labour seen in African mole-rat colonies, which sees breeders expending less energy foraging and digging while still having access to resources (SCANTLEBURY et al. 2006, FRANCIOLI et al. 2020, HOUSLAY et al. 2020, HART, BENNETT & SCANTLEBURY unpubl. data). Therefore, a female breeder’s body condition (a proxy for a surplus of energy) may be proportional to colony size (HOUSLAY et al. 2020, HART, BENNETT & SCANTLEBURY unpubl. data). This leads one to ask whether sociality, namely colony size, affects breeding seasonality in African mole-rats?

BREEDING IN AFRICAN MOLE-RAT

The reproductive strategy of 13 African mole-rat species, spanning the social spectrum in sub-Saharan Africa and representing all genera, has been investigated (see Fig. 1 and Table 2 for a summary). However, these studies are from single localities and may not represent the breeding strategies of the whole species across its distribution.

In general, breeding in all solitary and some social African mole-rat species is seasonal, with the activation of breeding coinciding with the increase in soil moisture content and the sudden flushes of primary production, which occurs as a consequence of the onset of rainfall (JARVIS 1969, BENNETT & JARVIS 1988a, BENNETT 1989, SPINKS et al. 1997, 1999b, JANSE VAN RENSBURG et al. 2002, HERBST et al. 2004, HART et al. 2006a). In contrast, most social and eusocial African mole-rats species breed throughout the year (BENNETT & JARVIS 1988b, BENNETT & AGUILAR

1995, OOSTHUIZEN et al. 2008, SICHILIMA et al. 2008, 2011, HART et al. 2021b). Interestingly, as mentioned above, all 13 species live in regions that experience some degree of seasonal rainfall (Fig. 1, Table 1); consequently, this may suggest that the seasonality of rainfall does not directly drive the seasonality of breeding in social African mole-rats species that form large colonies (Fig. 1).

In the past, links between ovulation mode and breeding strategy have been drawn (FAULKES et al. 2010), but recent findings have raised doubts about such links. For example, within the social and eusocial genera of *Cryptomys* and *Fukomys*, species that show aseasonal breeding can be either induced or spontaneous ovulators (MALHERBE et al. 2004, JACKSON & BENNETT 2005, BENNETT et al. 2010, FAULKES et al. 2010, HART et al. 2020b, VOIGT et al. 2021), therefore throwing doubt on the link between ovulation mode and breeding strategy.

Recent evidence, which has prompted this current hypothesis, suggests that an opportunistic breeding strategy may have been an ancestral state of African mole-rats (HART et al. 2006b, 2021b). As such, aseasonality and year-round positive energy balance, as seen in social and eusocial species that form large groups, is possibly brought about by the benefits of living in a cooperatively breeding group, while in the absence of sufficient cooperative help, solitary and social species that form small groups must restrict their breeding to times of a positive energy balance, the wet season.

SOCIALITY, COLONY SIZE AND SEASONAL BREEDING

Social and eusocial African mole-rats species with mean colony sizes usually greater than five individuals demonstrate an aseasonal reproductive pattern (Fig. 1). In contrast, the social species with mean colony sizes of five or less and all solitary species demonstrate a seasonal pattern of reproduction (Fig. 1). In species with mean group sizes greater than five individuals, the breeders, and in particular, females, possess year-round good body condition and a positive energy balance, likely due to year-round access to resources (food and water) and reduced frequency of engaging in strenuous activities, such as digging, due to the increased efficiency of locating and retrieval of resource as a function of group size. Within the African mole-rat family, this trend has been highlighted in *F. damarensis* by HOUSLAY et al. (2020), who demonstrated that the workload of breeding females falls disproportionately (relative to non-breeders), and their body condition during gestation and the size of their litter increases as group size increases. Furthermore, their inter-pregnancy interval declines while their fecundity increases (HOUSLAY et al. 2020) with colony size. However, this is not an uncommon trend in mammals that breed cooperatively, such as silver-backed jackals, *Canis mesomelas* (MOEHLMAN 1979), African wild dogs, *Lycaon pictus* (GUSSET & MACDONALD 2010, CREEL & CREEL 2015) and dwarf mongooses, *Helogale parvula* (ROOD 1990).

CONCLUSION, LIMITATIONS AND FUTURE DIRECTIONS

In conclusion, the ancestral breeding strategy of African mole-rats was likely opportunistic; therefore, breeding would occur year-round if a positive energy balance was maintained. In those species that were under environmental pressure to maintain (BURDA et al. 2000) or form larger colony sizes (JARVIS et al. 1994), a positive energy balance of the breeding females was maintained, through the benefits of living in a cooperatively breeding group, throughout the year independent on rainfall patterns resulting in an aseasonal breeding strategy. At the same

time, those species that maintained a solitary lifestyle (JARVIS et al. 1994) or became solitary (BURDA et al. 2000) or maintained small groups (HART et al. 2022a) had to rely on rainfall to achieve a positive energy balance and thus resulting in a seasonal breeding strategy. Regardless of which hypothesis of the evolution of sociality in African mole-rats (JARVIS et al. 1994, BURDA et al. 2000, HART et al. 2022a) you prescribe to, this current hypothesis, regarding the African mole-rat breeding strategy, fits into all. Furthermore, underlying phylogenetic causes are unlikely to drive breeding strategies in African mole-rats (Fig. 1); however, robust phylogenetic analyses are needed to substantiate this claim.

There are, however, current limitations to this hypothesis. First, this hypothesis is still in its infancy and needs to be rigorously tested in the field and challenged in the literature. The current literature, even though broad, is still too small to support our hypothesis truly; namely, the current studies are from single localities and may not represent the breeding strategies of the whole species across its distribution. Furthermore, these studies are often once-off observations (usually over a calendar year) and repeated observations on the same colony over numerous years, accounting for both changes in colony sizes and rainfall patterns are rare. Therefore multi-year studies monitoring reproductive readiness are needed on the same individuals to explore this hypothesis further. Seasonality of rainfall is a significant selection pressure for circannual breeding rhythms (breeding strategies). However, the circannual breeding rhythms can be controlled by several *zeitgebers*; as such future studies should focus on the seasonality of other environmental factors, such as humidity, soil moisture and temperature, food salinity, soil hardness, etc, while also using various databases. Furthermore, discussion and experimentation must address obvious questions, such as why African mole-rat species with a smaller colony size simply delay dispersal as an easy way to become aseasonal breeders? However, our initial thoughts on such a question are simply: individual fitness will always outweigh group fitness. African mole-rat species with a smaller family size live in conditions that promote dispersal (three water drops: more mesic, Fig. 1, Table 2). Therefore, non-breeders would not delay dispersal as their chance of successfully surviving away from their natal colony and starting a successful colony of their own is high. It may be beneficial for the breeding female to maintain colony sizes of above five individuals, but in mesic conditions, the non-breeders drive to reproduce and thus disperse would be so great that it would overcome reproductive suppression and the breeding female need for a larger colony. Therefore, the fitness benefit of breeding oneself (dispersing) would likely overcome the fitness benefit of remaining in the colony and performing cooperative care behaviours, overcoming the selection pressure of the breeding female to be an aseasonal breeder.

In summary, there is a strong link between group size and the seasonality of breeding in African mole-rats, a link that should be investigated in other group-forming mammals. However, rainfall patterns cannot be genuinely discounted as a driver of breeding strategy in African mole-rat, as rainfall patterns drive group size (Fig. 1).

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