

18 Senescence Patterns in African Mole-rats (Bathyergidae, Rodentia)

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18.1 Introduction

From an evolutionary viewpoint, senescence is an intriguing phenomenon. Many theories have been developed to identify its ultimate and proximate causes, but the process is so complex that, to date, barely any question about how and why organisms age has been fully answered. Consequently, even well-established theories on the evolution and mechanisms of senescence are still subject to research and debate.

For several reasons, African mole-rats of the family Bathyergidae are especially suited for aging studies. First, all members of the family are strictly subterranean and thus presumably suffer a lower risk of dying from predators or climatic extremes than surface-dwelling rodents. Since all relevant evolutionary senescence theories are based on the assumption that the rate of internal decay (i.e. senescence) is ultimately shaped by the extrinsic mortality risk (cf. e.g. Medawar 1952; Williams 1957; Kirkwood 1977), aging in mole-rats is predicted to be generally slow by these theories, making bathyergids very suited to test them. Second, in contrast to most other groups of subterranean mammals which are usually solitary (Nevo 1999; Burda et al. 2000), this family exhibits an exceptional diversity of social and mating systems, ranging from solitary and polygamous to social and monogamous species. Social and reproductive strategies are fundamental life history components and hence might affect longevity (as an integrative life history trait), too. The Bathyergidae therefore provide an interesting model to examine the influence of these factors on senescence. Third, the Bathyergidae are the only mammalian family known to date to include species with a truly eusocial organization, namely the naked mole-rat, *Heterocephalus glaber*, and several species of the genus *Fukomys* (*Fukomys* is a genus recently emancipated from the genus *Cryptomys* com-

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prising species of “*Cryptomys*” from out of South Africa; Ingram et al. 2004, Kock et al. 2006). Similar to hymenopterans and termites, colonies of these mole-rat species are characterized by monopolization of reproduction by few individuals (mostly a single breeding pair), reproductive altruism of their offspring (which involves non-breeding and cooperative alloparental brood care) and long-lasting philopatry resulting in an overlap of about six adult generations (Burda et al. 2000). Evolution of eusociality has led to a very peculiar aging-phenotype in eusocial insects, namely extreme longevity (some ant queens can live up to 30 years), caste-specific aging rates within species, and a complete reversal of the trade-off between reproductive investment and longevity (cf. Hölldobler and Wilson 1990) which is characteristic of most other organisms studied thus far (cf. Bell 1980; Stearns 1992). Since adoption of similar life styles often leads to convergence in life history traits (cf. Partridge 2001), the question arises whether eusociality is associated with similar aging characteristics in mole-rats, too.

Here we review what is known about senescence in bathyergid mole-rats, and add some new comparative aspects. Our goal is to integrate all these data in order to describe the aging phenotype of bathyergids comprehensively, i.e. on all taxonomic levels: interfamilial (comparing longevity of the family Bathyergidae to other rodent families), intrafamilial (comparing longevity of different genera and species within the Bathyergidae), and intraspecific (comparing aging rates of the reproductive and non-reproductive “castes” in eusocial species).

18.2

Longevity of Bathyergid Mole-rats Compared to Other Rodent Families

In mammals, longevity (expressed as maximum species life span, MLSP) is allometrically correlated with body size (Calder 1983; Promislow and Harvey 1990). We analyzed this relationship for rodents alone, both on the species and family level (see Fig. 18.1, where further details on data sources and methods are also provided). A simple rule of thumb to identify taxa with an extraordinarily high (or low) potential for longevity is provided by this allometry: the longer the distance from the regression line, the more exceptionally do the respective taxa age.

Amongst rodents, naked mole-rats *Heterocephalus glaber* have the highest MLSP for their body size: 28.3 years (Buffenstein and Jarvis 2002). As apparent from Fig. 18.1A, this remarkably high potential for long life span in relation to body size is characteristic not only for naked mole-rats, but also for other bathyergids. The Bathyergidae have the second highest MLSP for their body weight out of 26 analyzed rodent families, outranged

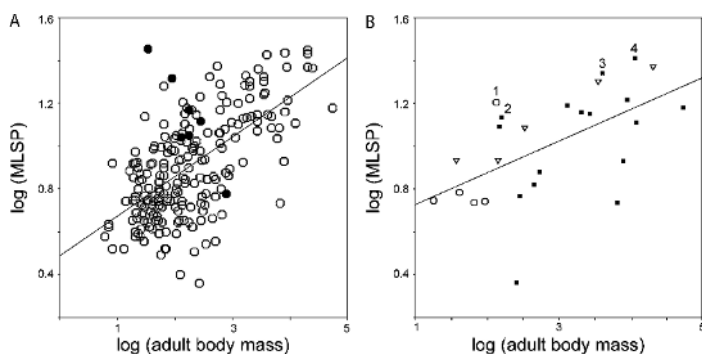


Fig. 18.1A–B. Maximum species life span (MLSP) and body mass in rodents. Data were obtained from our own recordings and Carey and Judge (2000), Weigl (2005), de Magalhães et al. (2005), Nevo, personal communication, Bennett, personal communication, and Jarvis, personal communication. Data declared as scarce, unreliable, incomplete, etc. were not included: **A** across species. *Filled circles*: bathyergid species ($n = 7$), *open circles*: species from other rodent families ($n = 205$). Body mass data are means over both sexes. The *regression line* is shown (linear regression after Pearson, $F = 135.54$; $df = 211$; $r^2 = 0.392$; $P < 0.0001$); **B** across families. *Circles*: Myomorpha ($n = 5$); *reversed triangles*: Sciuromorpha ($n = 5$); *filled squares*: Cavimorpha ($n = 16$; classification following Corbet and Hill 1980). Data on body mass and MLSP are means over all representatives of their respective families. The *regression line* is shown (linear regression after Pearson, $F = 11.17$; $df = 25$; $r^2 = 0.318$; $P = 0.003$). The four families with the longest life span relative to their body mass are numbered consecutively according to their distance from the regression line (in [brackets]: number of analyzed species per family): 1: Spalacidae [1], 2: Bathyergidae [7], 3: Erethizontidae [3], 4: Hystricidae [5]

only by the equally subterranean Spalacidae (Fig. 18.1B). Interestingly, the next two families exhibiting relatively long life span are the New and Old World porcupines (Erethizontidae and Hystricidae). This is in accordance with evolutionary aging theories, because most members of these families have evolved effective predator avoidance mechanisms, either ecologically (underground shelter) or morphologically (spines). Effect of phylogeny has to be considered particularly in this case because all of the mentioned rodent families but the Spalacidae belong to the suborder Hystricognatha. However, the hystricognath families are equally distributed above and below the regression line (cf. Fig. 18.1B) so that a phylogenetical bias does not seem to be the reason of the observed high MLSP.

One proximate cause of the aging process can be accumulated damage of biomolecules, cell components and tissues caused by reactive oxygen species (ROS) which are inevitably produced in the mitochondria as a side product of aerobic metabolism (“oxidative stress”, e.g. Finkel and Holbrook 2000). Therefore, in fossorial and subterranean species, it is interesting to speculate that long-term living in an atmosphere with low oxygen pressure

might reduce the negative effects of oxidative stress, providing a mechanistic rather than an evolutionary explanation for their relatively slow aging rates. However, the longevity records for spalacid and bathyergid mole-rats in Fig. 18.1 have been obtained in the laboratory, i.e. in relative hyperoxia compared to the natural situation. Under these conditions, naked mole-rats exhibit higher levels of oxidative stress than mice in all biomolecules measured so far (i.e. lipids, proteins, and DNA; Andziak et al. 2004, Buffenstein 2005). Naked mole-rats do not seem to have superior antioxidant defences compared to mice neither (Andziak et al. 2005). The authors concluded that it is unlikely that antioxidant defences are responsible for the eight-fold longevity difference between laboratory mice and naked mole-rats. While it would definitely be of interest to test whether oxidative stress in mole-rats under natural conditions (i.e. in the hypoxic atmosphere of their burrows; see also Burda et al., this volume) is lower than in the laboratory (making thus higher antioxidant defence not necessary), it is nevertheless apparent that – at least in naked mole-rats – antioxidant activities are not limiting factors in aging and/or that the naked mole-rats are highly tolerant of oxidative damage (Buffenstein 2005). Comparable studies on other long-lived mole-rat species would be highly informative but are not yet available.

18.3 Intrafamilial Longevity Patterns

Within the family Bathyergidae, the typical positive relation between body size and longevity (see above) is absent. Instead, the pattern is literally reversed: the smallest species (*Heterocephalus glaber*) has the highest and the largest species (*Bathyergus suillus*) the shortest MLSP for its size, respectively, leading to a strong negative correlation between body size and maximum life span within this family whose computed statistical values are highly significant (Fig. 18.2). This is interesting, but probably incidental and not causal: there is little reason to believe that body size per se had the opposite effect on longevity in bathyergids than in all other mammals. Thus, other factors must be taken into account.

Figure 18.2 suggests that social bathyergids (genera *Heterocephalus*, *Cryptomys*, and *Fukomys*) live longer than the solitary species (genera *Bathyergus*, *Georychus*). So the question arises: do sociality and/or monogamy promote longer lives in this family? Theoretically, both traits have the potential to reduce individual extrinsic mortality under certain circumstances and thus might be causative sensu evolutionary senescence theories (see above). For example, all else being equal, sociality should reduce individual predation risk by buffering exposure to predators (Alexan-

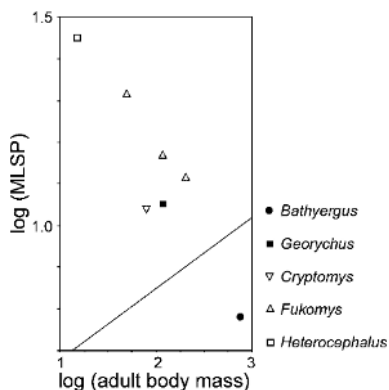


Fig. 18.2. Maximum species life span (MLSP) and body mass within the Bathyergidae. All genera that make up the family are represented except *Heliophobius*, since data on longevity are too preliminary for this genus (Šumbera, personal communication). *Filled symbols*: solitary/polygamous species; *open symbols*: social/monogamous species. The computed values of a linear regression analysis are: $F = 31.7$; $df = 6$; $r^2 = 0.318$; $P = 0.002$, but the corresponding regression line is not shown because the negative correlation between longevity and body mass is probably not causal (see text). Instead, the *regression line* for all rodent species (see Fig. 18.1A) is shown for orientation

der 1974; Ebensperger 2001). Among the few species which may prey on subterranean mammals, in sub-Saharan Africa the most common are the mole-snake *Pseudaspis cana* and (in some areas) the African striped weasel (*Poecilogale albinucha*). Both actively enter the burrow systems, and then probably attack the first burrow inhabitant they randomly encounter. Supposing that snakes and weasels usually kill only one prey individual per hunting event, it is evident that a mole-rat living in a group is less likely to be the particular individual met by the invader than a solitary burrow inhabitant who can hardly avoid this confrontation.

Another aspect is that the risks and costs of mate search must differ between polygamous and monogamous species that form stable pair bonds, because the former have to find a mate each year, whereas the latter do so only once in a lifetime. Reproductive dispersal and mate search are associated with substantial survival costs in many mammalian species (Stearns 1992) and are thought to be particularly costly for subterranean mammals, no matter whether they take place underground (high energetic expenditure of digging) or at the surface, where subterranean animals are surely more vulnerable to predators than surface-dwellers due to their limited locomotor and sensory abilities.

Furthermore, breeders in strictly monogamous *and* social species (*Fukomys*, *Heterocephalus*, *Cryptomys*; but only very few other mammals) should enjoy decreasing costs of mate competition as their family grows, presuming that their (adult) offspring behaves xenophobic against invading conspecifics and thus forms a “protective workforce” – not only against predators, but also against potential same-sex-rivals. This is the case for all social bathyergids (cf. Bennett and Faulkes 2000). Decreasing mortality risk with advancing age should therefore be characteristic of social mole-rats (because colony size increases), whereas in the solitary species

there is no reason to assume such age-dependency of environmentally imposed costs and risks, at least not after the animals are fully grown. All this matches very well with the seemingly slower aging rate of the social bathyergids.

It has to be noted that empirical data and theoretical calculations (cf. Burda et al. 2000 and references cited therein) suggest higher extrinsic mortality and group-turnover in *Heterocephalus* than in *Fukomys* mole-rats, despite *Heterocephalus* lives in much larger groups (cf. Bennett and Faulkes 2000 and references therein). Thus, among the social bathyergid species, group size per se does not necessarily reduce mean individual mortality risk, which seems to contradict the assumption of a straightforward effect of sociality on internal aging rate. However, as we will discuss in more detail in the following section, there is evidence from wild mole-rat colonies that breeders and non-breeders (“workers”) are exposed to differential risks due to “caste-specific” behavioural differences. Therefore, high colony turn-over and comparatively high predation risk for one subgroup (frequent workers) does not exclude that members of another subgroup can live extremely long once they have abandoned these risky tasks for one or the other reason. In accordance with that, in the social species the longevity record is regularly held by a breeding animal, not a worker (Buffenstein and Jarvis 2002; Dammann 2006; Dammann and Burda 2006).

However, one must keep in mind that there is a strong bias towards the social species in our knowledge and in availability of comparative data. Whereas thousands of individuals of naked mole-rats (and several hundreds in some *Cryptomys* and *Fukomys* species) have been maintained in various laboratories during the last 30 or 20 years, respectively, the interest in study and captive husbandry of their solitary counterparts has been triggered only recently. Thus, in a study of Sherman and Jarvis (2002), longevity data of 1140 naked mole-rats were analyzed. “Only” 86 (= 7.5%) of them lived longer than 15 years, 52 (= 4.6%) lived longer than 20 years. (However, note that Buffenstein 2005 stated that “if one excludes data from terminal experiments or human negligence, more than 80% of our original animals lived longer than 24 years in “captivity”, without, however, providing further details on sample size.) For comparison, systematic maintenance of solitary silvery mole-rats (*Heliophobius argenteocinereus*) in the laboratory has started less than ten years ago and the total number of captivity-kept individuals has not exceeded a few dozen (cf. Šumbera et al., this volume). Thus, based just on statistical grounds and on length of research, even if the silvery mole-rats had a similar longevity potential as the naked mole-rats, we have had little chance to find it out so far.

In conclusion, there are good indications that social and mating characteristics might affect aging in bathyergids, but a final answer to this question has to be postponed until more data for the solitary, polygamous species became available.

18.4

Intraspecific Aging Rates in Eusocial Bathyergids

Using long-term breeding data of a eusocial bathyergid species, the Ansell's mole-rat *Fukomys anselli*, we could recently demonstrate that reproductive division of labour goes along with a “caste”-specific aging pattern in this mammal. In fact, Ansell's mole-rat breeders of both genders lived approximately twice as long as their non-breeding counterparts. No difference was found between males and females in either reproductive caste. The oldest female breeder had lived for about 15 years when data collection was stopped; this female was still alive and reproducing. The longest lived male breeders had reached ages of about 20 years. In contrast, all non-breeders have died before their eighth birthday (Fig. 18.3).

The differences in aging rates were not due to variation in social rank, intrinsic quality, or time budgets allocated to feeding, resting, or working (Dammann and Burda 2006). Obviously, pair-bonding and/or sexual activ-

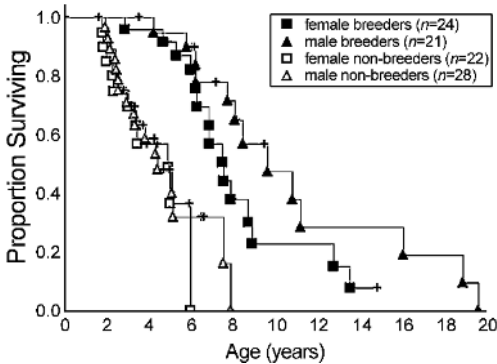


Fig. 18.3. Survival curves of breeding and non-breeding *Fukomys anselli*. Crosses indicate censored observations. Mean survival \pm SE, breeders: ♀♀: 8.3 ± 0.8 years, ♂♂: 11.1 ± 1.4 years; non-breeders: ♀♀: 4.3 ± 0.4 years, ♂♂: 4.8 ± 0.5 years. The differences were significant between breeders and non-breeders in both genders (log rank test pairwise over strata, ♀♀: $\chi^2 = 16.76$, $p < 0.0001$; ♂♂: $\chi^2 = 17.84$, $p < 0.0001$), but not between the genders in either reproductive caste (♀♀ vs. ♂♂ breeders: $\chi^2 = 2.92$, $p > 0.10$; ♀♀ vs. ♂♂ non-breeders: $\chi^2 = 0.08$, $p > 0.78$). Reprinted in changed form from Current Biology, Vol 16, Dammann and Burda, ‘Sexual activity and reproduction delay aging in a mammal’, pages R117–R118, Copyright (2006), with permission from Elsevier

ity and/or reproduction per se prolongs life in this species. *Fukomys anselli* thus is the first demonstration of a survival benefit of reproduction in a vertebrate. A very similar aging pattern has been found also in captive giant mole-rats (*F. mechowii*). Again, breeders lived on average approximately twice as long as non-breeders, whereas no difference was found between males and females within either reproductive “caste” (Dammann 2006). Hence, a reversal of the common trade-off between longevity and fertility seems to be characteristic of the genus *Fukomys*.

It still remains to be revisited what exactly goes on in *Heterocephalus glaber*. In this species, maximum longevity of breeding animals appears to equal that of non-breeders (Sherman and Jarvis 2002; Buffenstein 2005). Whether reproductive animals live *on average* longer than non-breeders, as is the case for *Fukomys*, is not known to date, because until now only data on maximum (and not mean) life span have been published.

18.5

“Caste”-Specific Aging: Possible Explanations

Do non-breeders have shorter lives than breeders, or do breeders live for longer than non-breeders? The shorter lives of non-breeders could be adaptive if longevity was traded against some other fitness trait. Since non-breeding mole-rats can maximize their inclusive fitness by either supporting their kin or founding a new colony elsewhere, they might invest less in somatic maintenance in order to maximize colony productivity and/or their own chances for successful dispersal, leading to a faster rate of aging.

In ants, higher workload in order to maximize colony productivity has been proposed as a proximate mechanism responsible for the more rapid senescence in workers (Tsuji et al. 1996; Hartmann and Heinze 2003). However, apart from engagement in sexual activity (it should be noted that breeding mole-rats copulate frequently and independently of any breeding cycle, Burda 1989, 1995) and pregnancy, parturition, and lactation in females there seem to be no substantial life style differences between captive *Fukomys* breeders and non-breeders (Dammann 2006; Dammann and Burda 2006). It seems therefore unlikely that a trade-off between workload and longevity is the cause for the differential aging rates we found, at least not on a simple wear and tear basis. It should however be pointed out that although the ultimate explanations refer to wild animals living under natural conditions, the longevity records and analyses of aging were done on animals living in captivity. Although the breeding and non-breeding mole-rats did not differ in their activities in our lab, there may be such differences in the field. Should the non-breeders under natural circumstances be the workers in the colony, they might spend more energy than

the breeders. Behaviourally one might see a difference only under natural conditions, not in captivity where food is provided *ad libitum*. It is not excluded however that the non-breeders maintain a larger or more energetical demanding metabolic apparatus (heart, liver, kidneys) which would subserve increased work rates in nature, but in captivity still contribute to increased metabolism. This preparedness for higher activity of non-breeders, which would be suppressed in breeders, might then lead to the significant survival differential observed in our study (Serge Daan, personal communication). However, times allocated to feeding do not suggest an increased energetic turnover in non-breeders. Also, our observations suggest that locomotor activity exhibited in captivity is an individually constant quantity which is not affected by availability or non-availability of food. It looks like as if there was a certain daily stint of work (locomotor activity, energy turnover) an animal does independently of availability of food. Surely, differential metabolism in animals of different sexes, ages, sizes, and breeding status has to be measured to recognize the role of energy turnover in determining the life span.

Besides colony productivity, non-breeding mole-rats might trade longevity against one or both of the other fitness traits, i.e. competitiveness in order to defend colonies against intruders or to enhance own chances for successful dispersal. In this context, it is interesting that when complete mole-rat colonies are trapped in the field, breeders are usually among the last individuals to be captured. This suggests that they are least likely to visit areas of potential danger in the burrow system, and that non-breeders are more prone to fulfil risky tasks such as burrow maintenance or colony defence (Bennett and Faulkes 2000). This tendency, besides protecting the colony, has also a selfish component because it enhances the chance to encounter potential mates from adjacent burrow systems. In all *Fukomys* species studied thus far, both sexes disperse (Bennett and Faulkes 2000), and mates are found either through random encounters of individuals from foreign burrow systems or active intrusion of other colonies in order to attain breeding status there (Spinks et al. 2000; Burland et al. 2004). The latter requires aggressiveness and competitiveness, which are also traits that improve defence performance against intruders. Investment in competitiveness might therefore be stronger in non-breeders than in breeders. Thus, if competitiveness somehow impairs somatic maintenance or repair, it would be a good candidate for an alternative trade-off faced more heavily by non-breeders. It is worth mentioning that in large, established laboratory colonies, most aggressive behaviour is initiated mostly by old non-breeders (often, but not always males; own unpublished data).

The second possible explanation, closely combining ultimate and proximate aspects, is that due to their peculiar mating system, mechanisms

might have evolved in social mole-rats which directly enhance life span in reproductive animals via mating and/or breeding. Breeders would then indeed live longer than non-breeders, not vice versa. Although very speculative at the moment, such a scenario would be in line with a prediction made by Schrempf et al. (2005) who recently showed that in the ant *Cardiocondula obscurior*, life span of queens is prolonged by mating and/or substances transferred via it. The authors introduced the term “sexual cooperation” for this phenomenon and predicted that it might not be restricted to social insects but could be found also in other animal taxa wherever partners show a lifetime commitment to each other. Schrempf et al. (2005) identified two preconditions favouring the evolution of sexual cooperation in ants: monogamy plus lifetime pair bond, and production of sexual offspring only after the colony has reached a certain size, i.e. a sterile work force has been established. Mole-rats belong to the few mammal species that meet the first criterion; furthermore, although all offspring are physiologically fertile, colony productivity and chances for the colony to survive increase with colony size (Jarvis et al. 1994). Thus, both partners profit from long-lived mates, as they ensure a high lifetime reproductive output. Any trait that helps enhancing the partner’s life span, e.g. transfer of antioxidants or other beneficial compounds through copulation, would therefore be under positive selection. It remains to be tested whether such traits have evolved in mole-rats and, if so, which kind they are.

Another important aspect is endocrinology. Sexual activity and pair bonding enjoyed by the breeding pair, but not by the non-breeders, is expected to result in surge of diverse hormones and neurotransmitters, particularly oxytocin, arginine vasopressin, sexual hormones, prolactin, dehydroepiandrostone, and dopamine (cf. Young and Wang 2004). These substances are known to have many positive effects and have been linked with enhancing immunity, reducing risk of cardiovascular diseases, reducing stress effects etc. (cf. Davey Smith et al. 1997). Referring to immunity, however, it should be noted that apparent infections or tumors were not causes of death recorded in our laboratory colonies. Therefore, it is at least questionable in how far the immunosuppressive or immuno-stimulating effects of certain hormones provide a proximate explanation for differential survival in the lab. Besides, it is possible that maturation and breeding in social mole-rats do not coincide with high secretions of the immunosuppressive steroids such as testosterone, corticosterone and progesterone. For example, serum testosterone and testes mass in males of mole-voles (*Ellobius talpinus*), a monogamous social species, are extremely low in comparison with other rodents (Novikov et al. 2004). Furthermore, no differences were found between breeding and non-breeding mole-voles in basal levels of serum and faeces corticosterone and in humoral immune

response (Moshkin et al., this volume; Moshkin personal communication). The authors suggested that in the (subterranean) species with low reproductive investment (K-strategists) there is no immune-reproductive trade-off. Analogous studies on some *Fukomys*-species are in progress.

18.6 Conclusions and Perspectives

African mole-rats (Bathyergidae) are suited to address questions about senescence both on the ultimate and the proximate level. Whereas more data on some understudied (solitary) members of the family are required in order to decide whether and how strong social and mating systems ultimately shaped intrinsic aging rates, the good knowledge and the relative ease of maintenance of the social species provides great opportunities already today. Due to their caste-specific aging pattern and their enormous potential for long life spans, eusocial insects have become model organisms for studying the proximate mechanisms underlying the aging process (e.g. Parker et al. 2004; Rueppell et al. 2005). However, extrapolation of results from insects to man is limited, especially on a physiological level. Therefore, for aging studies relevant to humans, the long-lived social bathyergids could become a valuable mammalian substitute. This is particularly true for the genus *Fukomys*, as these long-lived rodents offer the possibility to study differential aging rates within the same genetic configuration. In addition, in contrast to most Hymenoptera (and to some extent also in *Heterocephalus*), there are no morphological, behavioural or nutritional differences between reproductive and non-reproductive animals, which all might influence aging and complicate the identification of factors delaying or accelerating it. The best way to understand the aging process is to manipulate it (Davies 1983). In *Fukomys*, this can easily be done by giving the animals the chance to mate or not. Future studies should aim to elucidate potential changes in gene expression patterns, endocrine profiles, immune response and energy metabolism that might occur when an animal changes from non-breeding to breeding condition.

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