

## Analysis of ageing and longevity in African mole-rats – digging deeper than before (Rodentia: Bathyergidae)

Philip DAMMANN<sup>1,2</sup>, Sabine BEGALL<sup>1</sup> & Radim ŠUMBERA<sup>3</sup>

<sup>1</sup> Department of General Zoology, Faculty of Biology, University of Duisburg-Essen, Germany

<sup>2</sup> Central Animal Laboratory, Faculty of Medicine, University of Duisburg-Essen, Germany

<sup>3</sup> Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic

received on 26 October 2022

**Abstract.** African mole-rats (Bathyergidae) have intrigued gerontologists since extreme longevity and intraspecific divergence in ageing rates were demonstrated in some of their representatives. Although many ageing-related papers on African mole-rat species have been published in the last 20 years, a comprehensive overview of lifespan distributions, longevity metrics, and annual mortality rates in different mole-rat species (including solitary ones) is still lacking. In this paper, we aim to fill this gap by (re)analyzing published and hitherto unpublished longitudinal data of five African mole-rat species with different social organizations. We present strong indications that solitary mole-rats age faster than social species, and that the poorly studied Mashona mole-rat *Fukomys darlingi* exhibits some ageing characteristics not previously reported in other social mole-rats. Our study also provides the first overview of shape metrics of longevity for African mole-rat species intended to serve as a starting point for future updates.

**Key words.** Bathyergidae, ageing, lifespan, *Fukomys darlingi*.

### INTRODUCTION

African mole-rats (Bathyergidae) represent a monophyletic group of small to medium-sized rodents endemic to sub-Saharan Africa. The family consists of six recognized genera, all of which harbour species that live strictly underground in self-excavated burrow systems, feeding primarily on subterranean storage organs of plants that can be accessed without leaving their tunnels.

Two decades ago, the extreme longevity of one family member – the naked mole-rat *Heterocephalus glaber* – was reported (BUFFENSTEIN & JARVIS 2002, SHERMAN & JARVIS 2002), triggering a constantly growing interest in this family by gerontologists. This interest was reinforced by reports of highly divergent survival curves between reproductive and non-reproductive conspecifics in another social mole-rat species, the Ansell's mole-rat *Fukomys anselli* (DAMMANN & BURDA 2006, 2007). This trait, which appears to be characteristic of all *Fukomys* species (DAMMANN et al. 2011, SCHMIDT et al. 2013), made members of this genus valuable new model organisms for studying the mechanisms underlying ageing by providing a rare opportunity to study different rates of ageing within the same configuration of genes and under the same environmental conditions in individuals that appear to differ only in terms of pair bonding and sexual activity.

doi: 10.37520/lynx.2022.008

In addition to *Heterocephalus* and *Fukomys*, the family Bathyergidae includes four other genera exhibiting diversity of social and mating systems, ranging from solitary/polygamous to cooperatively breeding/monogamous species. This is in marked contrast to most other groups of subterranean mammals, which are normally solitary (NEVO 1999). In fact, half of the bathyergid genera are strictly solitary: *Bathyergus* (two recognized species), *Georychus* (one recognized species), and *Heliophobius* (currently one formally recognized species, but probably two species; see UHROVÁ et al. 2022), while the other half contains exclusively cooperatively breeding species: *Cryptomys* (five recognized species according to MONADJEM et al. 2015, but only one according to LACHER et al. 2016), *Fukomys* (14 recognized species sensu MONADJEM et al. 2015, plus an as yet undefined number of additional cryptic species, see VAN DAELE et al. 2007), and the monotypic genus *Heterocephalus*. Knowledge of longevity and ageing patterns is very unevenly distributed within the Bathyergidae. While the aforementioned social genera *Heterocephalus* and *Fukomys* have been studied thoroughly and in detail, other family members have been rather neglected by the gerontological community. The frequently used AnAge data base (TACUTU et al. 2018) currently lists seven African mole-rat species and reports maximum longevity records for six of them (i.e. <30% of all species in the family). These datasets were recently expanded by DAMMANN et al. (2022), who compiled updated longevity records for a total of nine African mole-rat species (six social and three solitary), albeit with large differences in sample size and thus reliability.

Apart from maximum longevity, which is the most widely used but also problematic longevity metric because of its high susceptibility to bias when sample sizes are small (RONGET & GAILLARD 2020), more detailed information about the distribution of age at death has only been published for three social mole-rat species (*F. anselli*: DAMMANN & BURDA 2006, DAMMANN et al. 2019; the giant mole-rat *F. mechowii*: DAMMANN et al. 2011, BEGALL et al. 2021; *H. glaber*: RUBY et al. 2018) and one solitary species, the silvery mole-rat *Heliophobius argenteocinereus* (DAMMANN et al. 2022). All of these publications reported Kaplan-Meier survival curves and mean and/or median life expectancy in addition to maximum longevity. However, only one (DAMMANN et al. 2022) had additionally calculated shape metrics such as 90% longevity (i.e., the age at which 90% of individuals had died) or scaled life expectancy (median survival divided by 90% longevity). Mortality hazards have so far been analyzed in detail only for *H. glaber* (RUBY et al. 2018) and *F. mechowii* (BEGALL et al. 2021), although for the latter in a highly specialized context (orphaned vs. non-orphaned non-reproductive animals).

The aim of this paper is to (re-)analyze published and previously unpublished datasets on survival and longevity of five African mole-rat species to provide a comprehensive overview of mortality patterns and longevity metrics, including calculation of mortality rates and shape metrics of longevity that have so far been missing from most studies on ageing in bathyergids.

## MATERIALS AND METHODS

### D a t a s e t s

We updated and reanalyzed published longitudinal data on lifespan and survival of Ansell's mole-rats *Fukomys anselli* (social; DAMMANN et al. 2019), giant mole-rats *Fukomys mechowii* (social; BEGALL et al. 2021), and silvery mole-rats *Heliophobius argenteocinereus* (solitary; DAMMANN et al. 2022). In addition, we analyzed hitherto unpublished longitudinal survival data for social Mashona mole-rats *Fukomys darlingi* and solitary Cape mole-rats *Georychus capensis*. Data for *F. darlingi* were obtained from our own husbandries in České Budějovice/Czech Republic and Essen/Germany, which are linked in that hus-

bandry conditions are comparable and animals are regularly exchanged between the two sites. Lifespan data for *G. capensis* were compiled and provided by Mary NOELL, Cincinnati Zoo/USA (pers. comm.), where a total of ten individuals were kept until natural death from 1987–1999. All of these studies have been conducted on captive animals. We did not use the published dataset for *H. glaber* (RUBY et al. 2018) due to an unfortunate statistical bias in this dataset (incomplete reporting of death events; for details see DAMMANN et al. 2019).

The published datasets used here differed slightly with respect to age of onset. For example, the published dataset for *Heliophobius argenteocinereus* contained lifespan distributions from birth, that for *F. anselii* from an age of entry of 0.5 years and that for *F. mechowii* from an age of entry of 1.5 years. Although mortality during this time interval is fairly low in all these species (own data), we standardised the datasets by setting the age of onset at one year for all species to make them comparable. This meant that for *H. argenteocinereus* and *F. anselii* we deleted data points from individuals younger than one year and updated the dataset of *F. mechowii* for individuals that had reached ages between 1 and 1.5 years. The latter updates were derived from our own ongoing breeding records of *F. mechowii*.

## Analysis of survival and longevity

In all survival analyses, the following conditions were treated as censored data points: the animal (a) was still alive at the time of census; (b) had been caught in the wild and age at the time of capture could not be estimated, e. g. based on the capture weight; (c) had been sacrificed for scientific studies; or (d) had died accidentally. We compared survival curves with a log-rank test using GraphPad Prism, Version 5. The following pace and shape metrics of longevity were derived from the survival data whenever possible: median longevity (life expectancy) at one year of age, maximum longevity (lifespan potential of the species), 90% longevity (i.e., the age at which 90% of the individuals in the dataset had died) and two measures of scaled life expectancy (median survival divided by (A) 90% longevity and (B) maximum longevity).

## Analysis of annual mortality rates

Annual mortality rates could be calculated for all species except *Georychus capensis*, as the initial sample size was too small for this species. For all other species, annual mortality rates were calculated by dividing the number of deaths of the respective species in the respective year of life by the sum of observation years for all individuals in the same interval. For social species, no distinction was made between reproductive (breeders) and non-reproductive animals (non-breeders) to allow comparison with the solitary silvery mole-rat. In each interval, individuals that lived throughout the interval contributed one year of observation time (or more than one year if intervals were expanded due to decreasing sample sizes; see below), while individuals that died or were censored during that interval contributed the time (expressed in years) until the death or censorship event. To account for decreasing sample size with advancing age, annual mortality was calculated for expanded intervals of more than one year after sample size has dropped below 20 individuals (applied only in the *Heliophobius argenteocinereus* data set; see Fig. 3).

Mortality hazards of the solitary and social species were compared by a repeated measures ANOVA with Dunnett's multiple comparisons post hoc test using *H. argenteocinereus* as reference for pairwise comparisons. The slopes of linear regression lines were calculated and compared with GraphPad Prism, Version 5.

## RESULTS

Survival proportions decreased faster in the solitary *Heliophobius argenteocinereus* and *Georychus capensis* than in all social species (Fig. 1A; log rank tests:  $p < 0.05$  in all pairwise curve comparisons between any solitary and any social species). Both solitary species also had considerably lower values of median and maximum lifespan compared to all social species (Table 1). Amongst the solitary species, *Heliophobius* outlived *Georychus* (log-rank test:

Table 1. Pace and shape metrics of longevity in five species of bathyergid mole-rats; med – median longevity (years) at one year of age; 90% – 90% longevity (years); max – maximum longevity (years); SLE-A – scaled life expectancy A: median / 90% longevity; SLE-B – scaled life expectancy B: median / max. longevity; n.a. – not applicable

metrics of longevity species (number of individuals)	pace			shape	
	med	90%	max	SLE-A	SLE-B
<i>Fukomys mechowii</i> (n=242)	10.23	20.92	26.10	0.49	0.39
<i>Fukomys anelli</i> (n=314)	9.58	20.19	21.50	0.47	0.45
<i>Fukomys darlingi</i> (n=110)	15.09	n.a.	18.02	n.a.	0.833
<i>Heliophobius argenteocinereus</i> (n=78)	7.92	14.54	14.62	0.55	0.54
<i>Georychus capensis</i> (n=10)	4.52	5.46	12.2	0.83	0.37

$p=0.0038$ ). Looking only at the social species, *F. anelli* and *F. mechowii* had fairly similar survival curves, yet *F. mechowii* showed higher survival at young ages and also reached a considerably higher maximum longevity. In contrast, the survival curve of *F. darlingi* had a much bulgier shape, indicating highest survival rates amongst all species under study in the first ca. 12 years, followed by a steep decline thereafter.

Within the social species, the survival benefit of breeders vs. non-breeders originally reported in *F. anelli* (DAMMANN & BURDA 2006) and *F. mechowii* (DAMMANN et al. 2011) is confirmed by our updated data (Fig. 1B). *Fukomys darlingi* shows a qualitatively similar pattern, yet the effect of reproductive activity on longevity appears to be less pronounced than in the other two *Fukomys* species and has a relatively high probability to be due to chance (log rank test,  $p=0.31$ ), probably due to the small sample size. In *F. mechowii* (females living longer) and *F. anelli* (males living longer), sex-specific differences in longevity could be observed, but this was not observed in *F. darlingi*. Also, in *H. argenteocinereus*, sex did not affect longevity. The effect of sex could not be analyzed in *G. capensis* as the information on sex was incomplete in this small dataset.

Life expectancy (median longevity) of *F. darlingi* was higher than in all other species, including *F. anelli* and *F. mechowii*, while maximum longevity was highest in *F. mechowii* (Table 1). *F. darlingi* also showed a higher value of scaled life expectancy (here: median/maximum lon-

Table 2. Actuarial senescence: main statistical parameters of a linear regression analysis between annual mortality rates and age. Positive slope values indicate increases of mortality with age, i.e. actuarial senescence. The higher the slope value, the faster is ageing

	<i>Fukomys anelli</i>	<i>Fukomys darlingi</i>	<i>Fukomys mechowii</i>	mean (social)	<i>Heliophobius argenteocinereus</i>
slope $\times 10^2$	0.5323	0.4997	0.8524	0.5576	2.853
95% CI $\times 10^2$	-0.065–0.110	-0.052–1.510	0.342–1.363	0.180–0.935	1.603–4.104
$r^2$	0.2393	0.2657	0.5513	0.49	0.8062
F	3.776	3.981	13.510	10.570	29.120
p	0.0758	0.0714	0.0037	0.0077	0.0010

geivity) than all other species, indicating that survival decreased rapidly between median and maximum longevity. *Georychus capensis* showed a high value for scaled life expectancy A, but a low value for scaled life expectancy B, probably due to the specific structure of this data set (see Discussion).

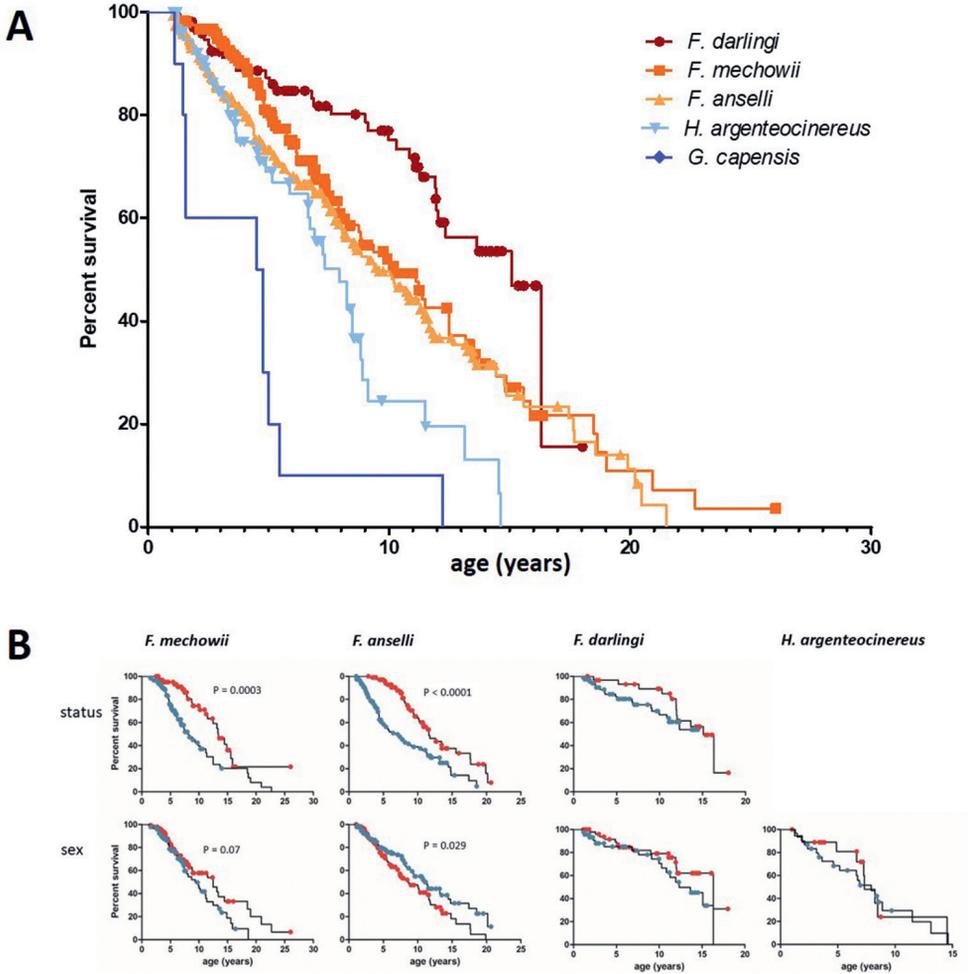


Fig. 1. Survival probabilities: symbols indicate right-censored data points. **A** – Kaplan-Meier curves for all five species under study (reproductive status and sexes combined, respectively). **B** – Breeders vs. non-breeders (first row; red = breeders), and females vs. males (second row; red = females). Curves were compared using log rank tests. Breeding status was not taken into account in *Heliophobius argenteocinerus* because in solitary mole-rat species, there is no clear-cut distinction between non-breeders and breeders as in the cooperatively breeding species. *Georychus capensis* is not depicted here because information about the sex of the individuals was mostly unavailable.

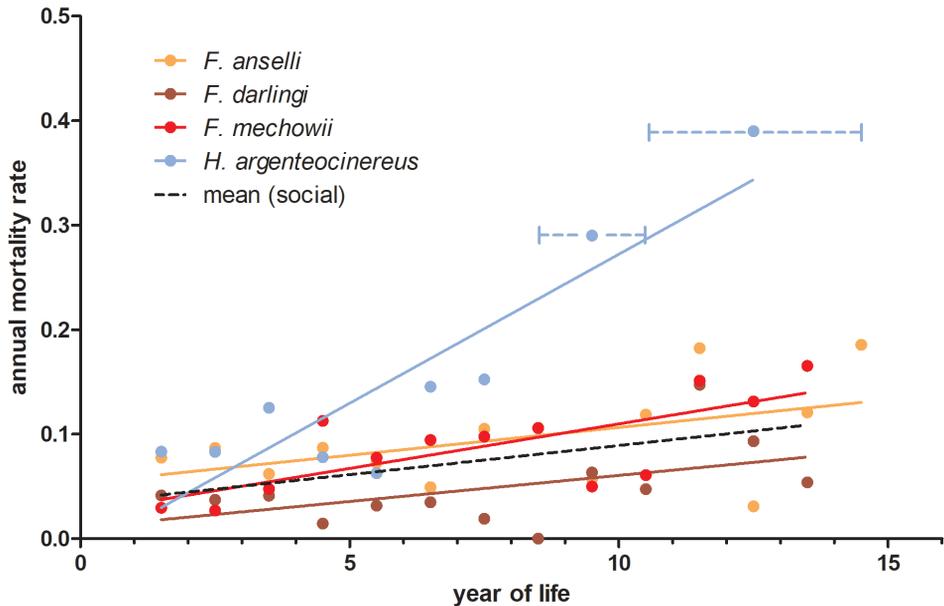


Fig. 2. Annual mortality rates: annual mortality rates (= number of recorded death events per observation year) of all species except *Georychus capensis* (above). Numbers on the x-axis represent consecutive years of life. To account for sample sizes dropping below 20 after the 8th year, years 9–11 and 12–15 were combined in *Heliophobius argenteocinereus*. Overall, slopes differed from each other ( $F= 8.582$ ,  $p<0.0001$ ). Over time, mortalities of the silvery mole-rat were higher than those of any social species (repeated measures ANOVA with Dunnett’s multiple comparison post hoc test: all  $p<0.05$ ).

The solitary *H. argenteocinereus* exhibited higher annual mortality rates and a steeper increase in this parameter than the social species (Table 2, Fig. 2). Of the social species, the mortality hazards were lowest in *F. darlingi* (Fig. 2). In all species, annual mortality increased with age, i.e. all species showed actuarial senescence (Table 2). This increase was highest in *H. argenteocinereus* and lowest in *F. darlingi* (Table 2).

## DISCUSSION

In the present study, we (re-)analyzed published and previously unpublished data on survival and longevity of three social and two solitary African mole-rat species. Our aim was to provide a comprehensive overview of mortality patterns and metrics of longevity in these species, including the calculation of mortality rates and shape metrics of longevity, which have been missing in most studies on ageing in bathyergids so far. These rates and metrics will allow future work to make appropriate comparisons within the Bathyergidae, rather

than comparing Bathyergidae to standard values published for distantly related species like e.g. *Mus* or *Rattus*.

According to our data presented here, the little-studied *Fukomys darlingi* from southern Malawi appears to show some ageing characteristics that have not been reported in other *Fukomys* mole-rats. Despite a relatively moderate value for maximum longevity, this species recovers the highest life expectancy (median longevity) among all *Fukomys* species analyzed so far. This is interesting because median longevity is much more robust against biases due to small sample sizes than maximum longevity (RONGET & GAILLARD 2020). Moreover, the maximum longevity reported here must be regarded as preliminary because more than 50% of the oldest individuals (>15 years) were still alive at the time of census, including the individual providing the current record. This species also shows the lowest mortality rates between 1 and 12 years of age among all species studied (but it has high pup mortality, ŠUMBERA et al. in press); however, the shape of the survival curves suggests that after ca. 12 years, annual mortality rates may increase more steeply than in other *Fukomys* species. Future work, with larger sample sizes in older age cohorts, will show whether this is true or not. In any case, it will be interesting to follow this species over a longer period of time to re-examine its lifespan potential, which may be considerably higher than indicated here. According to recent results, it seems that postnatal development of this social mole-rat is indeed slower compared to other social mole-rat species (ŠUMBERA et al. in press).

Our study also provides the first overview of shape metrics of longevity for different African mole-rat species. Our current data suggests that again, *F. darlingi* stands out in this respect, as the value of scaled life expectancy (here: median/maximum longevity) found in this species is much higher than in all other species. This metric illustrates the relative dispersion of mortality events over the lifetime of a population (RONGET & GAILLARD 2020). High values of this metric indicate that most individuals that reached an age older than the median longevity died within a relatively short period between the median longevity and the longevity metric in the denominator (here: maximum longevity). The relative dispersion of mortality is higher (i.e. the scaled life expectancy is lower) in all other species, which differ less from each other in this respect than all of them differ from *F. darlingi*. *Georychus capensis* is a special case, showing a high value for scaled life expectancy A, but a low value for scaled life expectancy B. This unusual pattern is most likely due to the small sample size in this dataset, coupled with the fact that the difference between the oldest individual and all other individuals is unusually high, resulting in a larger discrepancy between 90% and maximum longevity than for any other species. Like all other metrics reported here, the values of scaled life expectancies for *G. capensis* should be considered preliminary. Generally, our calculations of different longevity metrics of pace and shape are intended as a reference and starting point for further studies and updates in the future; its value will increase with higher sample sizes and longer observation times, especially for *F. darlingi* and other poorly studied social bathyergids (including *Cryptomys* sp.) as well as the solitary species from the genera *Georychus* and *Bathyergus*.

Finally, our data corroborate the assumption of THORLEY (2020) and DAMMANN et al. (2022) that sociality has a positive causal effect on the longevity of African mole-rats. DAMMANN et al. (2022) had already shown that social bathyergids consistently have higher median and maximum longevity than their solitary counterparts, and that the effect of sociality on longevity persists even after accounting for higher sample sizes in social species. Here, we substantiate these findings by showing that these differences in longevity are most likely caused by higher annual mortality rates and a steeper increase of this value with age (i.e. a higher ageing rate) in

the only solitary species, *Heliophobius argenteocinereus*, that could be analyzed in this respect. However, with the exception of this species, the data basis for solitary African mole-rats is still poor, so these results must be considered preliminary until they are verified with larger datasets.

## Acknowledgements

This work would not have come into being without the inspiration of Hynek BURDA, who sparked our interest in mole-rats especially through his early papers (BURDA 1989, 1990, 1992). As a teacher and mentor, Hynek always encouraged his scholars to pursue interesting findings whenever they came across. His breeding records of Zambian mole-rats, handwritten in the beginning and dating back to the 1980s, provided the starting point for all ageing studies on Zambian mole-rats that followed later, including this one. We therefore dedicate this paper to Hynek BURDA on the occasion of his 70th birthday.

We also thank Mary NOELL (Cincinnati Zoo) for providing longevity data for *Georychus capensis* and Stan BRAUDE for his helpful comments on an earlier version of this manuscript.

This study was supported by the Czech Science Foundation (GAČR 20-10222S).

## REFERENCES

- BEGALL S., NAPPE R., HOHREK L., SCHMIDT T. C., BURDA H., SAHM A., SZAFRANSKI K., DAMMANN P. & HENNING Y., 2021: Life expectancy, family constellation and stress in giant mole-rats (*Fukomys mechowii*). *Philosophical Transactions of the Royal Society London B: Biological Science*, **376**(20200207): 1–9.
- BUFFENSTEIN R. & JARVIS J. U., 2002: The naked mole rat – a new record for the oldest living rodent. *Science of Aging Knowledge Environment*, **2002**(21; pe7): 1–10.
- BURDA H., 1989: Reproductive biology (behaviour, breeding, and postnatal development) in subterranean mole-rats, *Cryptomys hottentotus* (Bathyergidae). *Zeitschrift für Säugetierkunde*, **54**: 360–376.
- BURDA H., 1990: Constraints of pregnancy and evolution of sociality in mole-rats. With special reference to reproductive and social patterns in *Cryptomys hottentotus* (Bathyergidae, Rodentia). *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, **28**: 26–39.
- BURDA H., 1992: Evolution of sociality in African mole-rats (Bathyergidae). *Zeitschrift für Säugetierkunde*, **57**, Supplement: 10–11.
- DAMMANN P. & BURDA H., 2006: Sexual activity and reproduction delay ageing in a mammal. *Current Biology*, **16**(4): R117–R118.
- DAMMANN P. & BURDA H., 2007: Senescence patterns in African mole-rats (Bathyergidae, Rodentia). Pp. 251–263. In: BEGALL S., BURDA H. & SCHLEICH C. E. (eds.): *Subterranean Rodents: News from Underground*. Springer, Berlin & Heidelberg, 416 pp.
- DAMMANN P., ŠUMBERA R., MASSMANN C., SCHERAG A. & BURDA H., 2011: Extended longevity of reproductives appears to be common in *Fukomys* mole-rats (Rodentia, Bathyergidae). *Public Library of Science One*, **6**(4, e18757): 1–7.
- DAMMANN P., SCHERAG A., ZAK N., SZAFRANSKI K., HOLTZE S., BEGALL S., BURDA H., KESTLER H. A., HILDEBRANDT T. & PLATZER M., 2019: Comment on ‘Naked mole-rat mortality rates defy Gompertzian laws by not increasing with age’. *eLife*, **8**(E45415): 1–6.
- DAMMANN P., ŠAFFA G. & ŠUMBERA R., 2022: Longevity of a solitary mole-rat species and its implications for the assumed link between sociality and longevity in African mole-rats (Bathyergidae). *Biology Letters*, **18**(20220243): 1–6.
- LACHER T., MITTERMEIER R. & WILSON D., 2016: *Handbook of the Mammals of the World. Volume 6. Lagomorphs and Rodents I*. Lynx Editions, Barcelona, 987 pp.
- MONADIEM A., TAYLOR P. J., DENYS C. & COTTERILL F. P., 2015: *Rodents of Sub-Saharan Africa: A Biogeographic and Taxonomic Synthesis*. Walter de Gruyter GmbH & Co KG., Berlin, 1102 pp.

- NEVO E., 1999: *Mosaic Evolution of Subterranean Mammals – Regression, Progression and Global Convergence*. Oxford University Press, Oxford, 413 pp.
- RONGET V. & GAILLARD J. M., 2019: Assessing ageing patterns for comparative analyses of mortality curves: Going beyond the use of maximum longevity. *Functional Ecology*, **34**: 65–75.
- RUBY J. G., SMITH M. & BUFFENSTEIN R., 2018: Naked mole-rat mortality rates defy Gompertzian laws by not increasing with age. *eLife*, **7**(e31157): 1–18.
- SCHMIDT C. M., JARVIS J. U. M. & BENNETT N. C., 2013: The long-lived queen: reproduction and longevity in female eusocial Damaraland mole-rats (*Fukomys damarensis*). *African Zoology*, **48**: 193–196.
- SHERMAN P. W. & JARVIS J. U. M., 2002: Extraordinary life spans of naked mole-rats (*Heterocephalus glaber*). *Journal of Zoology, London*, **258**: 307–311.
- ŠUMBERA R., UHROVÁ M., BEGALL S., CASPAR K. R., JERKOVIČOVÁ D., VAN DAELE P., CHITAU KALI W. N., FAULKES C. G., BENNETT N. C., JOHANNES C., BURDA H. & MIKULA O., in press: The biology of an isolated Mashona mole-rat population from southern Malawi, with implications for the diversity and biogeography of the genus *Fukomys*. *Organisms, Diversity and Distribution*.
- TACUTU R., THORNTON D., JOHNSON E., BUDOVSKY A., BARARDO D., CRAIG T., DIANA E., LEHMANN G., TOREN D., WANG J., FRAIFELD V. E. & DE MAGALHÃES J. P., 2018: Human Ageing Genomic Resources: new and updated databases. *Nucleic Acids Research*, **46**(D1): D1083–D1090.
- THORLEY J., 2020: The case for extended lifespan in cooperatively breeding mammals: a re-appraisal. *PeerJ*, **8**(e9214): 1–13.
- UHROVÁ M., MIKULA O., BENNETT N. C., VAN DAELE P., PÍÁLEK L., BRYJA J., VISSER J. H., JANSEN VAN VUUREN B. & ŠUMBERA R., 2022: Species limits and phylogeographic structure in two genera of solitary African mole-rats *Georychus* and *Heliophobius*. *Molecular Phylogenetics and Evolution*, **167**(107337): 1–17.
- VAN DAELE P. A., VERHEYEN E., BRUNAIN M. & ADRIAENS D., 2007: Cytochrome b sequence analysis reveals differential molecular evolution in African mole-rats of the chromosomally hyperdiverse genus *Fukomys* (Batherygidae, Rodentia) from the Zambezian region. *Molecular Phylogenetics and Evolution*, **45**: 142–157.