

Age-related dynamics of reproductive activity and physical conditions in Cricetidae of different ecological speciation (Rodentia)

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Abstract. To understand the evolutionary preconditions of extended longevity, one can compare the key life-history events and age related changes in body conditions in related species with different ecological speciation. Cricetid rodents possessing a wide spectrum of adaptive forms with different life history strategies are an excellent model for this purpose. We compared median and maximum longevity, life expectancy, temporal distribution of reproductive efforts, and age related dynamic of several physical condition indexes: body mass, muscle strength, locomotor activity and frequency of vertical postures in open field tests in five species of this family. Studied species vary both in maximum (from three years in steppe lemmings (*Lagurus lagurus*) to more than six years in mole voles (*Ellobius talpinus*) and rock voles (*Alticola strelzovi*) and median longevity (from less than one year in *Lagurus lagurus* to 2.8 years in rock vole *Alticola tuvinicus*). Both species with high maximum longevity – *Ellobius talpinus* and *Alticola strelzovi* face chronic hypoxia in their native environment. The total amount of litters born varied from three in *A. strelzovi* to 13 in *Phodopus sungorus*. Species under study also differed in age-related dynamics of physical conditions. Among the studied species, the subterranean *E. talpinus* has the highest maximum longevity with relatively long duration of reproductive period and only weak age-related deterioration in body conditions, i.e. shares many aspects of the life history strategy of such a specialized group as the Bathyergidae family.

Key words. Cricetidae, longevity, senescence, reproduction, muscle strength, activity.

INTRODUCTION

Rodents as a model group for gerontological studies have constantly attracted the attention of researches for the last several decades. High variability of life-histories, accompanied by extreme ecological and morpho-physiological diversity in addition with relatively easy capture and maintenance methods gave us unique opportunity to study inter-species differences within a broad spectrum of ontogenetic, behavioral and physiological traits that may contribute to the potential lifespan (GORBUNOVA et al. 2008). The different patterns of relations of such traits with the calendar and physiological age of individuals reflect the existence of different aging profiles (COHEN 2018). In some species, so-called “negligible senescence” phenomenon was described (FINCH et al. 1990). Among rodents there is at least one species considered to share this

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strategies – naked mole-rat (BUFFENSTEIN 2005, 2008). Although the uniqueness of this species is still a subject of discussion (BRAUDE et al. 2021), the importance of the subterranean way of life as an evolutionary precondition for slow aging and extended longevity is obvious (NEVO 1999, DAMMANN & BURDA 2007, NOVIKOV & BURDA 2013). To our knowledge, in all phyletic lineages that contain subterranean rodents, they live longer (with consideration of foraging habits, geographical distribution and body size) than related above ground species (DAMMANN & BURDA 2007, GORBUNOVA et al. 2008, DE MAGALHÃES & COSTA 2009). To reconstruct the evolutionary scenario which realized in different phylogenetic groups and to understand the proximate mechanisms of extended longevity and slow aging one should compare the life-history traits that affect lifespan in related species with different ecological speciation. Indeed, it would be preferable to include in such comparison the species that share at least some dimensions of the ecological niche of subterranean species. For example, to understand the role of the gas composition (low partial pressure of oxygen and high levels of carbon dioxide) not only burrowing, but also high-altitude species should be analyzed. Since the social way of life is discussed as an important evolutionary factor that favors the selection towards extended longevity (LUCAS & KELLER 2020), that is obvious at least for Bathyergidae family (DAMMANN & BURDA 2007, THORLEY 2020), comparative analyses should ideally include also species with different social organization – from solitary to pair-bonding and cooperatively breeding species.

One of the most serious issues in comparative biogerontological studies is the shaping of an adequate sample for the analysis. It is not easy to elaborate preliminary list of universal criteria for individuals belonging to different species, contrasting in lifespan and physiological senescence patterns. Uneven patterns of age-related dynamics of damage, caused by reactive oxygen species in the naked mole-rat and mice are a good example (ANDZIAK et al. 2005, ANDZIAK & BUFFENSTEIN 2006). One of the ways of solving this problem is the multi age-point approach that presumes the regular measurement of studied parameters during the whole, or at least a considerable cut of an individual's life cycle (ALTUN et al. 2007). The extreme points of the registered traits plotted on the temporal scale can give us appropriate information how they are related with other life-history events such as maturation, senescence or menopause. Unfortunately, such comparative studies (e.g. MORRISON et al. 1977) are still rare as they need a huge amount of time and resources for the maintenance of a sufficient number of live collections (especially for long lived species) for shaping a reliable sample for valid conclusions. Some nice examples of such studies give the works on the subterranean rodents of the family Bathyergidae, for a long time conducted by Hynek BURDA and his co-workers (DAMMANN & BURDA 2007, DAMMANN et al. 2011). One of the most interesting results of these studies concerns the unequal mortality patterns of reproducing and non-reproducing individuals of social mole-rat species (DAMMANN & BURDA 2006, DAMMANN et al. 2011). Fruitful collaboration with Hynek BURDA and his team (NOVIKOV & BURDA 2013, NOVIKOV et al. 2015a) gave us huge stimulus to spread such approach on the other rodent's group that we possessed in our laboratory – the Cricetidae family, that contains a wide spectrum of ecologically contrasted forms (PAVLINOV & LISSOVSKY 2012, KRYŠTUFEK & SHENBROT 2022). The maximum species lifespans (MLSP) registered in hamsters and voles are not as impressive as in mole-rats, but variable enough to be affected by ecological reasons (MORRISON et al. 1977, DE MAGALHÃES & COSTA 2009). On the other hand, MLSP do not describe the rate and shape of survival, which are essential for comparative analysis on population or species level (RONGET & GAILLARD 2020) so the complex of the metrics that generally characterize the aging process, such as median longevity, life expectancy, age of reproductive senescence etc. should be also considered.

During the last decade, we realized the multi age-point approach in comparisons of life history, behavioral and physiological traits of some species of Cricetidae family. New results of this project were regularly published (NOVIKOV et al. 2015b, 2017, 2019, 2020, 2022). Since the list of the species involved in this study has been updated and the number of completed observations has steadily increased, the release of new data remains relevant. The main question addressed in the paper presented here is whether there are species-specific patterns of physical and reproductive senescence in rodents of the Cricetidae family occupying different ecological niches. This publication gives us an excellent opportunity to congratulate Hynek Burda with his Jubilee and to illustrate the scale of his scientific contribution in modern biology.

MATERIAL AND METHODS

Animals

Our live collection of murid rodents contain species which inhabit steppe, forest and mountain landscapes of Siberia and has been maintained in the Laboratory of structure and dynamics of the populations of animals, Institute of Systematics and ecology of animals SB RAS for several decades. The total number of the species involved in different research programs exceeds 20, but among them the several species of the family Cricetidae are the objects of special interest. At present, representative material for comparative analysis of age-related dynamics of body condition has been collected for five species: the dwarf hamster (*Phodopus sungorus*) – a solitary, above ground, mainly granivorous species inhabiting semi-arid landscapes; the mole vole (*Ellobius talpinus*) – a cooperatively breeding subterranean species feeding of roots and rhizomes; the herbivorous steppe lemming (*Lagurus lagurus*) that live in pairs; and two species of rock voles – *Alticola tuvanicus* and *A. strelzovi*. The last two species inhabit rocks and stone placers, live in small social groups of closely related individuals, are mainly herbivorous, but differ in preferred altitudes: 400–800 m for *A. tuvanicus* and 1500–3000 m a. s. l. for *A. strelzovi* (PAVLINOV & LISOVSKY 2012, KRYŠTUFEK & SHENBROT 2022). As all these species successfully reproduce in the laboratory, both naturally-trapped and laboratory-born individuals have been involved in this study. To our knowledge, there is no common phylogenetic analysis yet including all studied species. The modern taxonomy refers dwarf hamsters to the Cricetinae subfamily whereas all other species are assigned to three different tribes of the Arvicolinae subfamily. Lagurini and Ellobini tribes belong to the ancient clade, more related to the Cricetinae subfamily than Clethrionomini tribe to which genus *Alticola* belongs (ROBOVSKÝ et al. 2008, KRYŠTUFEK & SHENBROT 2022).

Keeping conditions

All animals were maintained in comfortable conditions considering the ecological preferences of the respective species. In all species except the mole voles, the laboratory born animals were initially maintained in sibling groups, paired after attainment of maturity and kept in pairs until the death of one of the partners. Live-trapped individuals of social *Ellobius talpinus* were initially placed in groups of four (2 males + 2 females, individually marked by toe-clipping). Offspring were kept for some times with their parents, and then removed for the formation of new family groups. The cages were provided with layer (sawdust), nesting material (cotton), cuts of wood and bark as environmental enrichment and as a means for teeth sharpening. The cage sizes and construction provided free animal movements in all three dimensions. The diet composition varied according to the species preferences but always included fresh carrots, fruits, grain mixtures (oat, weed, sunflower), manufactured conventional rodent pellets and fresh herbs. Animals were fed three times a week. Fresh water was provided ad lib. While feeding the animals and cleaning, we examined the cages and recorded the cases for the occasions of birth and death. The number of the newborn pups was calculated on the day of birth.

Testing protocol

At the age of 4–6 months, each individual was tested for the first time using a standard protocol, including the recording of body mass, muscle strength measurement and 3 min open field test. Subsequently all individuals underwent the same tests every 6 months. Muscle strength was measured using the original dynamometer, which consisted of spring scales connected with a steel spring 4 cm in diameter placed in plastic tube. Tested animal was placed in the tube and fixed inside by front paws. Any attempt of the experimenter to withdraw the animal led to the shift of the scales proportionally to the force applied. The maximum value registered on the scales for a given animal in three attempts was taken as the individual muscle strength index. The standard open field test lasted for 3 min in a plastic arena with 50 cm in diameter which was divided into four sectors. Here we analyze two indexes, reflecting the different aspects of animal's activity in open field: Horizontal locomotor activity calculated as the number of sectors passed by the individual, and number of vertical postures that reflects the orientation reactions as a component of exploratory behavior.

Data treatment

Daily examination of the cages gave us the possibility to monitor directly all life history events from birth to death of laboratory born individuals. In order to avoid overestimation of real lifespan in naturally trapped individuals with unknown age, we considered all of them to be 30 days old in the moment of capture – the age when pups of small species of the family Cricetidae normally leave their maternal nests. To explore signs of aging, we calculated the mean sizes of successive litters in females and mean values of indexes reflecting the physical state of an individual: body mass, muscle strength, horizontal activity and number of vertical postures, measured at different ages with 6 month iteration. Each sample included all surviving individuals of a given species, so the sample sizes were uneven and inevitably decreased in consecutive

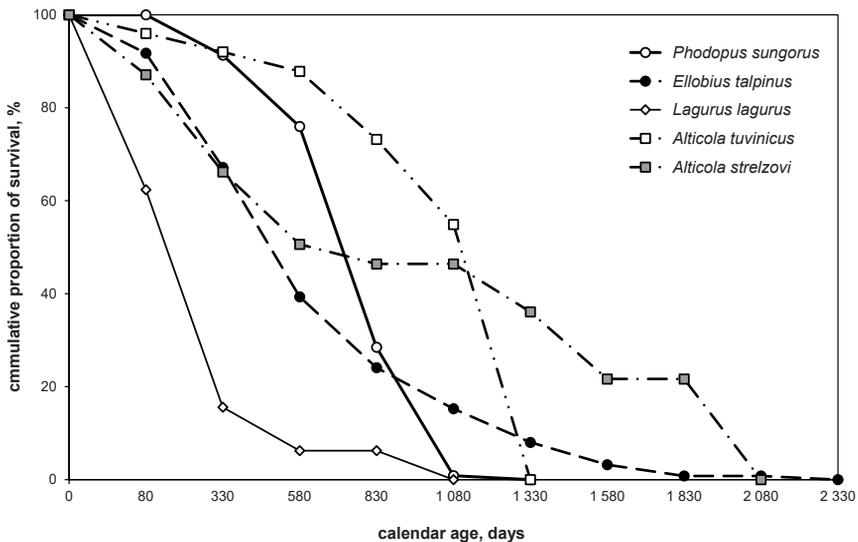


Fig. 1. Rate of survival in the five species under study. The cases of significant (log-rank test, $P < 0.05$) differences of mortality curves between species are marked by different letters.

Table 1. Basic life history traits of five rodents of the family Cricetidae; n – sample size; med – longevity, days, median; exp – life expectancy $\pm 95\%$ conf. limit, days; max – longevity, days, maximum; offspring birth (age, days, maximum / minimum); dur – duration of reproduction, days

species	n	med	exp	max	offspring birth		dur
					min	max	
<i>Phodopus sungorus</i>	72	974.0	904.8 \pm 56.8	1303	119	1039	920
<i>Ellobius talpinus</i>	133	676.0	794.5 \pm 75.2	2334	133	1320	1187
<i>Alticola tuvinicus</i>	25	1080.0	985.6 \pm 110.9	1511	329	837	508
<i>Alticola strelzovi</i>	32	627.5	786.1 \pm 186.9	2283	458	784	326
<i>Lagurus lagurus</i>	53	362.0	373.8 \pm 52.4	1110	71	630	559

tests. Here we did not apply the analysis of constant samples considering long-lived individuals only (NOVIKOV et al. 2015b, 2022), because such an approach restricts the time interval of valid observations and may obscure real trends in age – related dynamics. Animals that were still alive when this article was finished or occasionally died (due to the aggression of conspecifics or any accidents) were included in the analysis as censored observations. We applied standard statistical methods using Statistica 12.0 software. The maximum species lifespan (MLSP) was estimated as maximum value registered in the sample of a given species. Life expectancy was calculated as the mean lifespan of the individuals, attained reproductive conditions (RONGET & GAILLARD 2020). We used the Kaplan-Meier approach for analysis of survival curves. For pair comparisons we performed log-rank tests. The existence of age related trends in the values of studied indexes was examined using the significance (t-test) of linear regression coefficients.

RESULTS

The data presented in Table 1 show the considerable between-species variability both in median and maximum longevity. The MLSP of mole voles and rock voles was considerably higher than in other species; although median longevity and life expectancy were not drastically different among species. This controversy may be explained by the species-specific patterns of survival, which, with few exceptions, significantly differed among species (Fig. 1): the most long-lived species has relatively high mortality rates in first years of life.

The age of first successful childbirth considerably varied among species being the minimum for *Lagurus lagurus* and the maximum for the *Alticola* species. *Phodopus sungorus* and *Ellobius talpinus* had intermediate values of this index, equal approximately for six month. Maximum age of offspring appearance and, consequently, maximum total duration of reproductive period was registered for *E. talpinus*. Rock voles, despite their relatively high MLSP, had a low duration of reproductive period (Table 1). Respectively, the total amount of litters born was only three in *Alticola strelzovi*, but more than 10 in *P. sungorus* and *E. talpinus* (Fig. 2). In all species age-related decrease in litter size was more or less pronounced (Table 2).

Body mass remained relatively constant throughout life in *P. sungorus* and *A. tuvinicus*, increased in *L. lagurus* and *A. strelzovi* and decreased in *E. talpinus* (Fig. 3, Table 2). A negative age-related trend in muscle strength was clearly observed in *P. sungorus*, but was only weak in the other species (Fig. 4, Table 2). Locomotor activity in open field test decreased with age in *L. lagurus* only, and even increased in *E. talpinus* (Fig. 5, Table 2). The frequency of vertical postures had a downward trend in all species except rock voles but in *L. lagurus* this trend was insignificant (Fig. 6, Table 2).

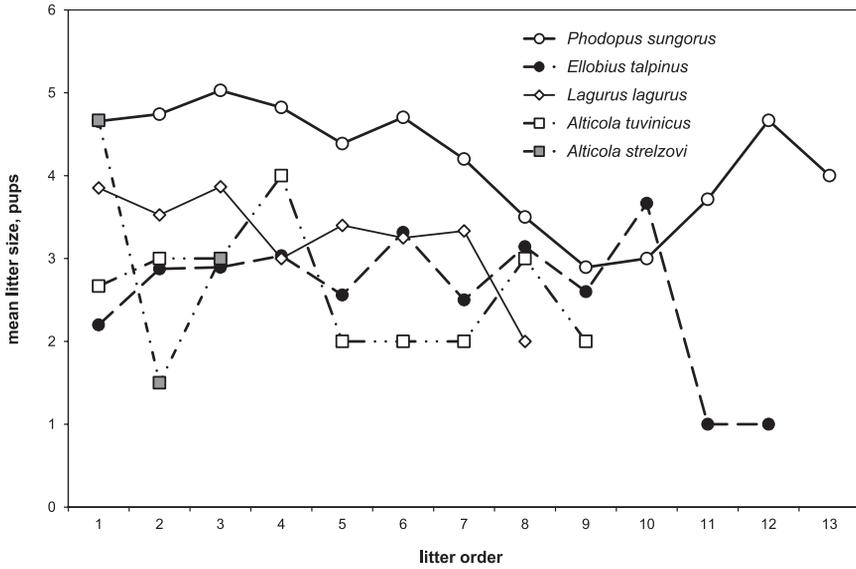


Fig. 2. Age-related dynamics (number of order) of litter size in females of the five species under study.

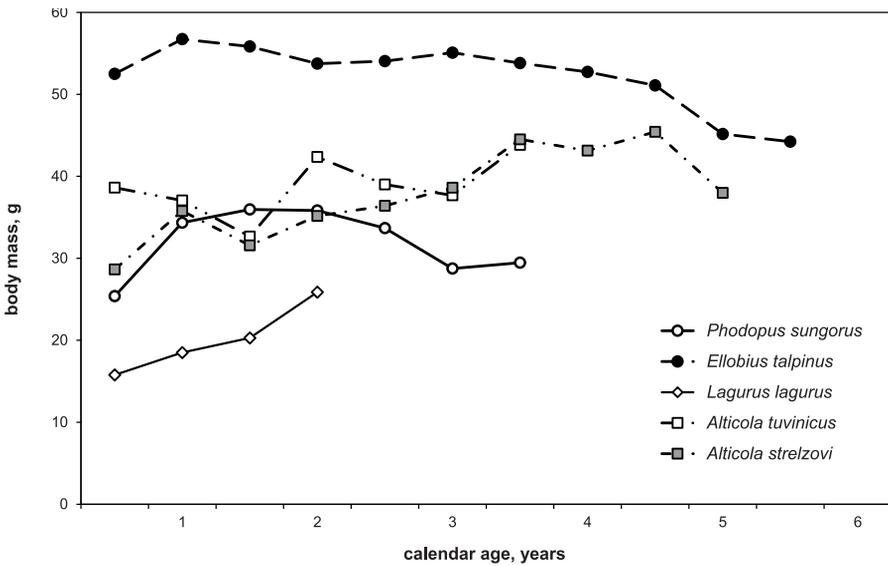


Fig. 3. Age-related dynamics of body mass of the five species under study.

Table 2. Age-related dynamic of indices, reflecting reproductive activity and physical conditions of five species of the Cricetidae family (equations of linear regression, significance of approximation). The cases of significant (Student t-test; $P < 0.05$) temporal trends are marked **bold**

species	litter size	body mass	muscle strength	horizontal activity	vertical postures
y <i>Phodopus sungorus</i>	-0.1057x	-0.044x	-7.6948x	-0.4001x	-0.5975x
+	4.92	32.09	99.35	19.10	11.41
R ²	0.3396	0.0005	0.5674	0.141	0.6374
y <i>Ellobius talpinus</i>	-0.0906x	-0.9468x	-5.9433x	5.3719x	-1,2957x
+	3.15	57.95	339.68	49.35	20.20
R ²	0.1549	0.5972	0.1361	0.7117	0.5486y
y <i>Alticola tuvinicus</i>	-0.1111x	-0.1111x	7.1983x	0.1681x	-0.1021x
+	3.19	35.42	236.36	19.64	12.89
R ²	0.1911	0.2408	0.0624	0.0100	0.0033
y <i>Alticola strelzovi</i>	-0,8333x	1.4526x	-6.1888x	-0,2814x	-0.4821x
+	4.72	29.73	322.83	18.40	15.79
R ²	0.2768	0.6496	0.1563	0.0223	0.0537
y <i>Lagurus lagurus</i>	-0.1831x	3.209x	-10.438x	-3.8598x	-2.3925x
+	4.1023	12.09	70.21	29.59	17.50
R ²	0.5706	0.9418	0.2925	0.7887	0.5093

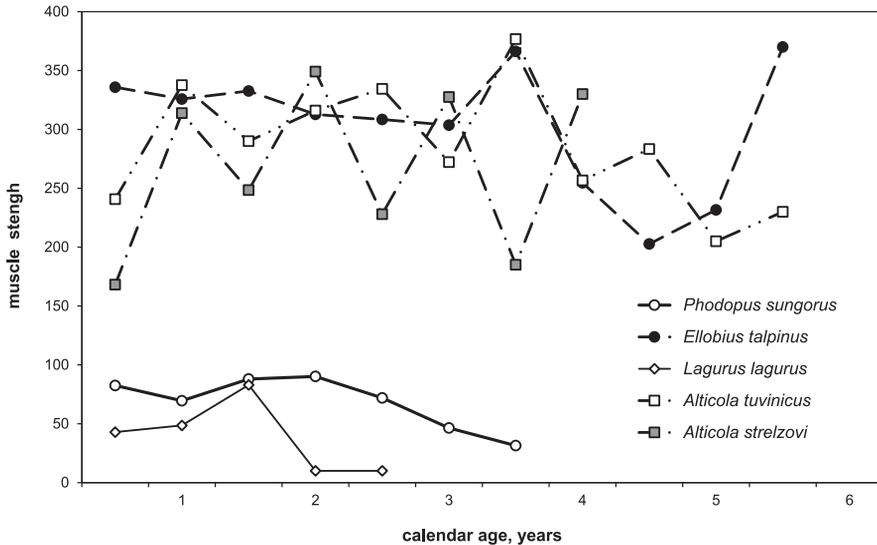


Fig. 4. Age-related dynamics of muscle strength of the five species under study.

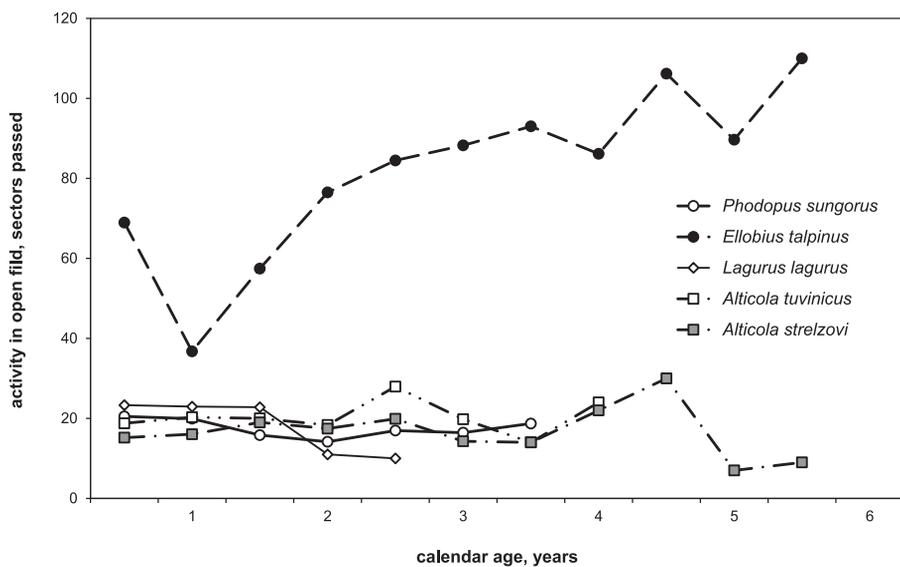


Fig. 5. Age-related dynamics of locomotor activity of the five species under study.

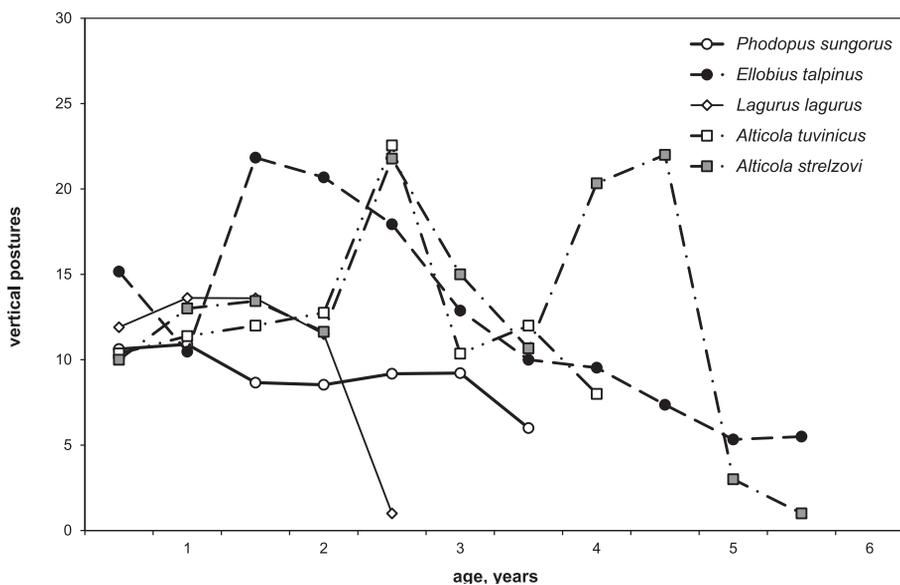


Fig. 6. Age-related dynamics of frequency of vertical postures of the five species under study.

DISCUSSION

The species under study belong to the same phyletic lineage (Cricetidae), occupy overlapping geographical ranges (southern Siberia), have comparable adult body mass (30–60 g), but inhabit different landscapes and occupy different (and even contrasted) ecological niches (PAVLINOV & LISSOVSKY 2012, KRYŠTUFEK & SHENBROT 2022). Since all of them inhabit open landscapes, they cannot be correctly ordinated in ecological scales such as aridity-humidity. On the other hand, the studied species drastically differ in preferred food (herbivorous – granivorous – omnivorous), social structure (solitary – social) and likelihood of exposition to abnormal atmospheric gas composition. Low partial oxygen pressure (hypoxia) associated with high carbon dioxide concentrations is a common challenge for the species that use the burrows as shelters in inactive period of diurnal cycle (*Phodopus sungorus* and *Lagurus lagurus*), and especially – for subterranean species (*Ellobius talpinus*). Rock voles, inhabiting mainly stone placers, may also be exposed to chronic hypoxia the severity of which depends on the altitude above sea level. Climatic conditions (winter severity, snow cover depth, soil temperatures) are also expected to affect adaptive features of each species. It is these dimensions of the ecological niche – climate, food habits, shelter and gas composition in the atmosphere – as well as the social and mating systems that attract the attention of evolutionary ecologists when they try to explain the variability in morphofunctional traits and life history traits between species.

The restricted samples (especially for rock vole species, some of which are still alive) allow us to make only preliminary conclusions now. But it is obvious that even in the five species under study, some key life-history events vary considerably during lifetime. Primarily one can see significant differences in life expectancy, median longevity and MLSP. Interestingly these parameters do not tightly correlate with one another. At least in two species – *Ellobius talpinus* and *Alticola strelzovi*, MLSP appears to be considerably higher than it is typical for murid rodents and that can be expected on the base of allometric relations with body mass. These two species have comparable body size but contrast in their ecological preferences. The only niche dimension that is common for both but not for other species is oxygen partial pressure in inhaled air. Chronic hypoxia has been discussed as one of several evolutionary preconditions for extended longevity in subterranean species (BUFFENSTEIN 2005, DAMMANN & BURDA 2007, NOVIKOV & BURDA 2013, SCHMIDT et al. 2017). Interestingly, the related species, *Alticola tuvinicus*, which prefer low to moderate altitudes, have lower MLSP than *A. strelzovi*. On the other hand, the life expectancy and median lifespan of species with high MLSP appear to be even lower than in *P. sungorus* and *A. tuvinicus*. Respectively the mortality curves of the two last species were more “rectangular” than those of *E. talpinus* and *A. strelzovi*, in which only a small proportion of individuals had a lifespan at least twice as long as the species median. The high level of mortality among juvenile and non-reproductive individuals was described in social bathyergids (BUFFENSTEIN 2005, DAMMANN & BURDA 2006, DAMMANN et al. 2011) and seems to be a common life-history trait for subterranean social species (NOVIKOV & BURDA 2013, NOVIKOV et al. 2015b). Besides the species-specific survival patterns high mortality of long-lived species may be caused by their lower tolerance to keeping conditions (NOVIKOV et al. 2022). This phenomenon illustrates the importance of the complex approach to the description of survival patterns (RONGET & GAILLARD 2020) and seems to be very interesting from the point of view of practical gerontology and animal welfare.

Another interesting conclusion that follows from our study is the absence of a correlation between the age of maturation, duration of reproductive period and MLSP, which reveals from the meta-analysis of large scale (DE MAGALHÃES et al. 2007). We did not fix the time of attaining

maturity when shaping the reproductive pairs, so the data concerning the age of first litter appearance should be interpreted carefully. Nevertheless, in rock voles age of first litter appearance was significantly higher than the age of pairing. Both in laboratories and in natural populations these species normally reproduce only in the second year of life and usually bring only a few litters per lifetime (list of references see in NOVIKOV et al. 2022). On the other hand, the most long-lived species, *E. talpinus*, is comparable in this respect to *P. sungorus* which has a far shorter MLSP. Combination of relatively early maturation with large duration of reproductive period contradicts the predictions of the pace-of-life theory (RICKLEFS & WIKELSKI 2002) and seems to be peculiar for social subterranean rodents (BUFFENSTEIN 2005, 2008), regardless the taxonomic differences in absolute values of MLSP and pregnancy duration.

Another possible subject of discussion is the considerable difference between the age of the last litter and MLSP. Reproduction of females usually terminated far earlier than their male mates deceased. This period, which can be characterized as “reproductive senescence” also varies among the rodents under study, being maximal in species with high MLSP – *E. talpinus* and *A. strelzovi*. The impressive duration of this period (more than half of MLSP) in laboratory-caged rodents give us the possibility to clarify the evolutionary role of senescence and to elaborate the criteria for highlighting the occasions of senescence in wild populations of animals (NUSSEY et al. 2013).

The most interesting perspective for geriatric applications of comparative studies with multi age-point approach, performed on animal models, is the temporal scaling of the processes, associated with age-related deterioration in reproductive function and body conditions. Our study revealed the spectrum of the temporal patterns in the dynamics of such vital characteristics as litter size, body mass, muscle strength, locomotor activity and exploratory behavior – traits that determinate the physiological, physical and emotional state of an individual and act as markers of senescence. Specifically, body mass and grip strength are known to be good predictors of the residual lifespan in humans (RANTANEN et al. 2000, LEONG et al. 2015). Age-related changes in physical and physiological conditions, examined in our study, differed both among species and among indexes. In *P. sungorus* and *L. lagurus* litter sizes steadily decreased with the order number of litter. An age-related loss of body mass was detected in *E. talpinus* only. Muscle strength gradually decreased with age in *P. sungorus*. Locomotor activity in open field test remained stable or even increased in all species except *L. lagurus*, frequency of vertical postures significantly decreased with age in *E. talpinus* and *P. sungorus*. For rock voles, that inhabit three-dimensional space of stone placers, vertical postures seems to be an essential component of foraging and exploratory behaviors so frequency of its manifestation remains stable almost all over their entire life. Species-specific rate of age deterioration seems to be associated more closely with MLSP than with median longevity or other life history traits. In the short-lived *L. lagurus* and *P. sungorus*, signs of deterioration appear already in their second year of life. In *E. talpinus*, like in social bathyergids (DAMMANN & BURDA 2006, DANMMANN et al., 2011), survival strongly depends on the reproductive status of the individual. Most non-breeders usually disappear from the population in the first-second years of life, whereas breeders both in laboratory and in nature can survive for six years. The data presented here shows that in actively reproducing individuals the first signs of senescence appear at the age of four years, when reproductive activity is normally terminated (NOVIKOV et al. 2015b).

Generally, one can conclude that among the species under study, the social and subterranean *E. talpinus* excels the other species regarding MLSP, duration of reproductive period and ability to maintain high level of physical and physiological conditions over lifetime with minimal

signs of deterioration. These features are far more expressed in other convergent group – social subterranean rodents of the family Bathyergidae (DAMMANN & BURDA 2007). A potential role of the soil as a medium in the generating a selective force towards the slow aging and extended longevity is evident but it is not easy to reveal the relative impact of different ecological factors in this process. Similarity of some life history and morpho-physiological traits of mole voles and rock voles suggest the important role of adaptations to chronic hypoxia in the evolution of extended longevity.

Due to the relatively short period of observations on the restricted laboratory stocks of several species and inevitable reduction of sample sizes with age, now we can make only preliminary conclusions on the topic of the study. Primarily it is the case for estimation of MLSP (RONGET & GAILLARD 2020) and other indexes that strongly depends on the sample size. But already the first results of our study illustrate the scales of variability of the life history traits among the phylogenetically related species presumed to be an adaptive response on the environmental challenges.

A c k n o w l e d g e m e n t s

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REFERENCES

- ALTUN M., BERGMAN E., EDSTRÖM E., JOHNSON H. & ULFHAKE B., 2007: Behavioral impairments of the aging rat. *Physiology & Behavior*, **92**: 911–923.
- ANDZIAK B. & BUFFENSTEIN R., 2006: Disparate patterns of age-related changes in lipid peroxidation in long-lived naked mole-rats and shorter-lived mice. *Aging Cell*, **5**: 525–532.
- ANDZIAK B., O'CONNOR T. P. & BUFFENSTEIN R., 2005: Antioxidants do not explain the disparate longevity between mice and the longest-living rodent, the naked mole-rat. *Mechanisms of Ageing and Development*, **126**: 1206–1212.
- BRAUDE S., HOLTZE S., BEGALL S., BRENMÖHL J., BURDA H., DAMMANN P., DEL MARMOL D., GORSHKOVA E., HENNING Y., HOEFLICH A., HÖHN A., JUNG T., HAMO D., SAHM A., SHEBZUKHOV Y., ŠUMBERA R., MIWA S., VYSSOKIKH M. Y., VON ZGLINICKI T., AVERINA O. & HILDEBRANDT T. B., 2021: Surprisingly long survival of premature conclusions about naked mole-rat biology. *Biological Reviews*, **96**: 376–393.
- BUFFENSTEIN R., 2005: The naked mole-rat. A new long-living model for human aging research? *Journal of Gerontology A*, **60**: 1369–1377.
- BUFFENSTEIN R., 2008: Negligible senescence in the longest living rodent, the naked mole-rat: Insights from a successfully aging species. *Journal of Comparative Physiology B*, **178**: 439–445.
- COHEN A. A., 2018: Aging across the tree of life: The importance of a comparative perspective for the use of animal models in aging. *Biochimica et Biophysica Acta (BBA) – Molecular Basis of Disease*, **1864**: 2680–2689.
- DAMMANN P. & BURDA H., 2006: Sexual activity and reproduction delay ageing in a mammal. *Current Biology*, **16**: 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. (eds): *Subterranean Rodents – News from Underground*. Springer, Heidelberg, 398 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.
- DE MAGALHÃES J. P. & COSTA A. J., 2009: A database of vertebrate longevity records and their relation to other life-history traits. *Journal of Evolutionary Biology*, **22**: 1770–1774.
- DE MAGALHÃES J. P., COSTA J. & CHURCH G. M., 2007: An analysis of the relationship between metabolism, developmental schedules, and longevity using phylogenetic independent contrasts. *Journal of Gerontology, Series A: Biological Sciences and Medical Sciences*, **62**: 149–160.
- FINCH C. E., 1990: *Longevity, Senescence, and the Genome*. University of Chicago Press, Chicago, 922 pp.
- GORBUNOVA V., BOZZELLA M. J. & SELUANOV A., 2008: Rodents for comparative aging studies: from mice to beavers. *Age*, **30**: 111–119.
- KRYŠTUFEK B. & SHENBROT G. I., 2022: *Voles and Lemmings (Arvicolinae) of the Palaearctic Region*. University of Maribor, Maribor, 449 pp.
- LEONG D. P., TEO K. K., RANGARAJAN S., LOPEZ-JARAMILLO P., AVEZUM JR. A., ORLANDINI A., SERON P., AHMED S. H., ROSENGREN A., KELISHADI R., RAHMAN O., SWAMINATHAN S., IQBAL R., GUPTA R., LEAR S. A., OGUZ A., YUSSOF K., ZATONSKA K., CHIFAMBA J., IGUMBOR E., MOHAN V., ANJANA M., GU H., LI W. & YUSUF S., 2015: Prognostic value of grip strength: findings from the Prospective Urban Rural Epidemiology (PURE) study. *The Lancet*, **386**: 266–273.
- LUCAS E. R. & KELLER L., 2020: The co-evolution of longevity and social life. *Functional Ecology*, **34**: 76–87.
- MORRISON P., DIETERICH R. & PRESTON D., 1977: Longevity and mortality in 15 rodent species and sub-species maintained in laboratory colonies. *Acta Theriologica*, **22**: 317–335.
- NEVO E., 1999: *Mosaic Evolution of Subterranean Mammals: Regression, Progression, and Global Convergence*. Oxford University Press, Oxford, xxvi+413 pp.
- NOVIKOV E. A. & BURDA H., 2013: Ecological and evolutionary preconditions of extended longevity in subterranean rodents. *Biology Bulletin Reviews*, **3**(4): 325–333.
- NOVIKOV E. A., KONDRATUK E. Y. & BURDA H., 2015a: Age-related increase of urine cortisol in non-breeding individuals of *Fukomys anselli* (Rodentia, Bathyergidae) from a laboratory colony. *Zoologičeskij Žurnal*, **94**(1): 119–124.
- NOVIKOV E., KONDRATUK E., PETROVSKI D., TITOVA T., ZADUBROVSKAYA I., ZADUBROVSKIY P. & MOSHKIN M., 2015b: Reproduction, aging and mortality rate in social subterranean mole voles (*Ellobius talpinus* Pall.). *Biogerontology*, **16**: 723–732.
- NOVIKOV E., ZADUBROVSKAYA I., ZADUBROVSKIY P. & TITOVA T., 2017: Reproduction, ageing and longevity in two species of laboratory rodents with different life histories. *Biogerontology*, **18**: 803–809.
- NOVIKOV E., KONDRATUK E., TITOVA T., ZADUBROVSKY P., ZADUBROVSKAYA I., POTAPOV M., POTAPOVA O., PROSKURNYAK L. & NAZAROVA G., 2019: Reproduction and mortality rates in ecologically distinct species of murid rodents. *Biogerontology*, **20**: 149–157.
- NOVIKOV E. A., KONDRATUK E. Y. & POLIKARPOV I. A., 2020: Age-related differences in physiology and survival of northern red-backed voles (*Myodes rutilus*) in captivity. *Biogerontology*, **21**: 133–142.
- NOVIKOV E. A., LOPATINA N. V., TITOVA T. V., ZADUBROVSKIY P. A. & LITVINOV Y. N., 2022: Physical condition, activity, and longevity of two rock vole species: *Alticola tuvinicus* and *A. strelzowi*. *Proceedings of the Zoological Society (Kolkata)*, **75**: 103–110.
- NUSSEY D. H., FROY H., LEMAITRE J. F., GAILLARD J. M. & AUSTAD S. N., 2013: Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. *Ageing Research Reviews*, **12**: 214–225.
- PAVLINOV I. Y. & LISSOVSKY A. A., 2012: *The Mammals of Russia: A Taxonomic and Geographic Reference*. KMK Scientific Press, Moscow, 604 pp.
- RANTANEN T., HARRIS T., LEVEILLE S. G., VISSER M., FOLEY D., MASAKI K. & GURALNIK J. M., 2000: Muscle strength and body mass index as long-term predictors of mortality in initially healthy men. *Journal of Gerontology Series A: Biological Sciences and Medical Sciences*, **55**(3): M168–M173.

- RICKLEFS R. E. & WIKELSKI M., 2002: The physiology/life-history nexus. *Trends in Ecology & Evolution*, **17**: 462–468.
- ROBOVSKÝ J., ŘIČÁNKOVÁ V. & ZRZAVÝ J. 2008: Phylogeny of Arvicolinae (Mammalia, Cricetidae): utility of morphological and molecular data sets in a recently radiating clade. *Zoologica Scripta*, **37**: 571–590.
- RONGET V. & GAILLARD J. M. 2020: Assessing ageing patterns for comparative analyses of mortality curves: Going beyond the use of maximum longevity. *Functional Ecology*, **34**: 65–75.
- SCHMIDT H., MALIK A., BICKER A., POETZSCH G., AVIVI A., SHAMS I. & HANKELN T., 2017: Hypoxia tolerance, longevity and cancer-resistance in the mole rat *Spalax* – a liver transcriptomics approach. *Scientific Reports*, **7**(1): 1–13.
- THORLEY J., 2020: The case for extended lifespan in cooperatively breeding mammals: a re-appraisal. *PeerJ*, **8**(e9214): 1–13.