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What Determines the Life Span of a Species?

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Abstract—Diverging in the initial assumptions, both mechanistic and evolutionary theories of aging suggest a positive correlation of indicators of life expectancy of animal species with body size and a negative correlation with fertility and metabolic rate. Such dependence is obviously traced within large taxa; however, when analyzing on a smaller scale (at the level of orders and families), ecological specialization of species can make a significant contribution to the variability of the corresponding indexes. In given work, correlative relationships between median and maximum life expectancy, on one hand, and the average values of body weight, fertility, muscle strength, the values of standard and maximum metabolic rates, locomotor activity, and emotionality in the open field test, on the other hand, are analyzed in eight species of Cricetidae family. The correlations with life expectancy were significant for all indicators except body weight. For locomotor activity, the correlation with life expectancy was positive; for other indicators, it was negative. The paper discusses possible reasons for differences in the strength of correlative relationships of the analyzed indexes with the maximum and median life expectancy from the point of view of mechanistic and evolutionary approaches to the analysis of the causes and mechanisms of aging.

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INTRODUCTION

The question of the causes and mechanisms of aging goes far beyond the scope of practical gerontology. The study of the variability in the life span of animals and the reasons for it is one of the central problems of modern evolutionary biology. To explain the causes of aging as a phenomenon that is clearly maladaptive from the point of view of an individual organism, a large number of different theories have been proposed, which can generally be divided into two main groups: mechanistic theories and evolutionary theories (Goldsmith, 2011). The former proceed from the obvious position that selection loses its effectiveness as residual fertility declines with age and cannot influence the aging process. Stochastic accumulation of random failures in the operation of various systems associated with transcription errors, the damaging effect of oxygen free radicals, loss of elasticity of cell membranes, and other irreversible biochemical processes are considered as possible causes of age-related deterioration in the state of the body, which ultimately leads to irreversible consequences (Harman, 1956; Gavrilov and Gavrilova, 1991; Speakman et al., 2002). It is assumed that the rate of such processes and, consequently, the rate of aging of the body are directly related to the intensity of energy metabolism (Pearl, 1928; Kleiber, 1932). Modern evolutionary theory of aging based on the concept of r and K selection (Pianka, 1974) suggests that, at the species level, both the total life span and the duration of individual stages of ontogeny are determined by the probability of premature death of individuals from random causes. Under the conditions of inevitable competition for resources between reproductive and somatic functions in nature, the contribution to the offspring is more profitable from the point of view of fitness than the contribution to the somatic maintenance and reparative processes. Therefore, after reaching puberty, the body's resources are re-allocated mainly in favor of the reproductive function, which makes the aging process and death of the body inevitable. The high risk of death of animals from random causes contributes to the evolutionary trend toward accelerated puberty and more intensive reproduction with a smaller parental contribution to each offspring. Therefore, large and well-protected species owing to ecological or morphological adaptations live longer than small animals easily accessible to predators (Kirkwood, 1977; Kirkwood and Rose, 1991). An analysis of a large amount of data showed the existence of a close relationship between the life span of animals and their body weight and age of maturity, in the absence of a correlation with residual (normalized to body weight) values of basal metabolism. Cases of species falling out of the expected allometric patterns are a good illustration of the evolutionary theory of aging. Thus, among mammals, life expectancy is higher than expected, on the basis of the regression dependence on body weight, in bats and primates (Magalhaes et al., 2007), i.e., well-protected species with a low risk of premature death from extrinsic causes (Gorbunova et al., 2008). At the same time, the patterns that are clearly seen in the analysis of large taxa are not always realized at the level of families, especially such specialized ones as, for example, mole-rats (Bathyergidae). Small social species of this family live much longer than solitary large ones (Dammann and Burda, 2007).

The reciprocal relationship between somatic and generative functions underlying current evolutionary theories suggests an inverse relationship between life span and reproductive costs (Kirkwood, 1977; Kirkwood and Rose, 1991). This dependence is well traced, in particular, in bats (Wilkinson and South, 2002). Unfortunately, there are very few comparative works on the analysis of reproduction costs and life expectancy at the species level. When analyzing the trade-off relationships between somatic and reproductive functions in animals from natural populations, the question inevitably arises: (1) Is their reciprocal nature associated with direct competition for limited resources, or (2) is it a consequence of evolutionary constraints imposed by the action of natural selection, which optimizes the allocation of these resources between functions? Obviously, in the first case, indexes reflecting the state of reproductive and somatic functions will be subject to significant intraspecific variability, reflecting the uneven influence of environmental factors, and correlate (depending on the pattern of age-related mortality dynamics) with the average or median (if the distribution of life expectancy differs from normal) life expectancy of individuals of the studied species. In the second case, we should expect a close relationship between the state of individual functions and the maximum life expectancy, as a stable species characteristic formed in the process of natural selection. However, in the natural habitats, the identification of such patterns is hampered by the uncontrolled contribution of mortality from extrinsic causes (weather disasters, diseases, and predators), so it is advisable to use in gerontological studies animals kept under standard laboratory conditions.

Unfortunately, there are practically no comparative works in the world literature in which the indexes of the functional activity of the vital functions of an organism in different species would be analyzed from the standpoint of the variability of their life span. It would be preferable to carry out such work on representatives of the same phyletic lineage, in order to avoid the influence of different evolutionary histories of species. On the other hand, to identify interspecies variability in life span and functional activity of various systems of the body, it is advisable to use an ecologically contrasting taxonomic group in which the studied parameters would differ quite strongly in different species. In this regard, rodents of the Cricetidae family could become a very convenient group, demonstrating a wide range of life forms (Bashenina, 1977; Pokrovsky and Bolshakov, 1979). However, practically the only work on a comparative analysis of life span and factors influencing it in species of this family, representing various adaptive types and phyletic lineages, under standardized conditions of keeping is the study by Morrison et al. (1977).

The maintenance in our laboratory of a living collection of murid rodents living in the south of Siberia made it possible to perform a comparative analysis of life expectancy and characteristics that reflect the functional state of various systems of the body, aimed at understanding the causes that determine life expectancy at the species level. To achieve this goal, we considered the correlation relationships between life expectancy and species-specific values of indicators reflecting various aspects of the vital activity of the body, trying to reveal the nature of the observed correlations.

MATERIALS AND METHODS

Representatives of eight species of murid rodents of the Cricetidae family served as material for the work: the Djungarian hamster (*Phodopus sungorus*), northern mole-voles (*Ellobius talpinus*), steppe lemmings (*Lagurus lagurus*), and water (*Arvicola amphibius*), narrow-skulled (*Lasiopodomys gregalis*), red-backed (*Myodes rutilus*), Tuvan (*Alticola tuvinicus*), and flat-headed (*A. strelzovi*) voles. The water vole, the largest of the considered species, lives along the banks of water basins, feeding on near-water vegetation; the Dzungarian hamster, steppe lemming, northern mole vole, and narrow-skulled vole inhabit arid (forest-steppe and steppe) habitats. The Dzungarian hamster is a predominantly granivorous species with a large proportion of animal food in the diet, the narrow-skulled vole and the steppe lemming feed mainly on green vegetation, and the northern mole vole feeds on underground parts of plants. The red-backed vole prefers forest and taiga habitats, feeding mainly on plant seeds. We used both individuals caught in nature at a young age and kept in the laboratory for the rest of their lives, as well as their descendants of one or two generations.

Over the past ten years, animals of these species have been periodically caught with live traps. Young immature animals were delivered to the laboratory, where they were kept in cages 40 × 30 × 20 cm (mole-voles in round enclosures 50 cm in diameter) at a temperature of 18–22°C. The photoperiodic regime was changed in accordance with the natural change in illumination: 8L : 16D in winter, 12L : 12D in spring and autumn, 16L : 8D in summer. Feeding conditions depended on the characteristics of the biology of the species: seed-eating species were given factory-made feed for rodents (Vaka, Zhorka), a grain mixture (oats, sunflower seeds) with the addition of pine nuts and berries was given to red-backed voles, animal feed (meat, boiled egg, flour worms) was given to Djungarian hamsters, and green-eating species were given fresh herbs, hay, and carrots. Mole-voles were offered mainly fresh carrots with the addition of other root crops and a grain mixture. All animals were supplemented with apples and factory-made granular conventional feed (Chara K°). Young animals of all species (with the exception of the northern mole-vole) were kept singly or in sibling groups; upon reaching puberty, pairs were formed, which remained until the death of one of the partners. Individuals of the northern mole-vole, sharing a colonial way of life in nature, were kept in groups of four individuals (two males and two females), weaning offspring as they matured. Inspection of the cells was carried out daily, the facts of the birth of offspring and the death of animals were recorded. The number of offspring born was counted at birth and after cessation of lactation. The dead animals were examined and autopsied to identify injuries or pathologies that were a possible cause of death.

As an indicator of the maximum life span of a species, we used the maximum of the values recorded by us for the entire period of observation of this species. The values obtained did not differ significantly from those available (but not for all species) in the literature (Magalhaes and Costa, 2009) or they exceeded them. Since the distribution of life expectancy did not obey the normal law for all the considered species owing to pronounced right-sided asymmetry (Kolmogorov–Smirnov test; $P < 0.05$), median survival was used as a measure of laboratory survival. Reproductive activity was assessed by the average brood size recorded for this species in our observations. This indexes, on one hand, adequately reflects the current costs of reproduction and, on the other hand, in contrast, for example, to the total number of offspring born during a lifetime, is little susceptible to random observation errors. As indicators reflecting the state of somatic functions, we considered body weight, muscle strength of the forelimbs, basal metabolic rate, maximum (cold) metabolic rate, and behavioral repertoire demonstrated in the open field test. Daily registration of the facts of the birth of offspring made it possible to estimate the age of animals born in the laboratory with an accuracy of one day. In the calculations of survival curves, only individuals with a life span of more than a month were used, since at this age the rodents of most of the studied species leave the nests and begin to lead an active lifestyle. The calendar age of wild-caught animals at the time of capture was taken equal to one month in order to avoid overestimation of the maximum life span.

Muscle strength was analyzed using an original design setup, which consists of a dynamometer (Pesola C° spring balance with a scale limit of 1 kg) fixed on a stationary base and connected to a plastic cylinder 5 cm in diameter, in which the test animal was placed. In order for the animal to be fixed in the cylinder with its front paws, a steel spiral was placed inside. After fixing the animal in the cylinder, we took it by the back of the body and tried to remove it from the cylinder, which was displaced along the longitudinal axis of the installation, setting the dynamometer scale in motion. The maximum scale shift recorded before the animal opened its paws was considered an indicator of its muscle strength (Novikov et al., 2015c). Because of the difference in the sizes of the tested animals, muscle strength was considered in the analysis as specific values, relating it to body weight.

To measure the values of the standard (resting metabolic rate in the thermoneutral zone, an indexes close in value to the basal metabolic rate) and maximum metabolic rates , we used the method of indirect calorimetry in a closed-type respirometer (Kalabukhov, 1951) in a modification designed in our laboratory and repeatedly described earlier (Novikov et al., 2015b, 2021; Polikarpov et al., 2016; Zadubrovsky et al., 2021). The outsized dimensions and capabilities of the test equipment did not allow us to correctly assess the metabolic rate of the water vole.

The interspecies variability of the behavioral repertoire was assessed by the results of the standard open field test (Hall, 1934, 1936). The behavior of the northern mole-vole turned out to be extremely monotonous: the animals constantly moved along the wall of the test arena and showed almost no other behavioral acts. Because of doubts about the validity of the open field test for this species, which lives in the one-dimensional space of underground passages, it was excluded from the analysis. Data for other species were combined into a single sample, which was processed using component analysis (Zadubrovsky et al., 2017, 2021). The most significant contribution to the first principal component, which explains 19.4% of the variability, was made by indexes of vertical and horizontal activity (the number of sectors passed in the center and on the periphery of the arena, the frequency of vertical stances). The second component, explaining 11.2% of the variance, was formed mainly by the frequency of defecations and the number of boluses left during the test (Table 1), which, in accordance with the classical interpretation of the results of the open field test proposed by its author Hall (Hall, 1934, 1936), was considered as a manifestation of the emotionality of animals. The values of the first and second components, averaged for each species (sample centroids), were used as species characteristics of locomotor activity and emotionality in a comparative analysis.

To assess the statistical significance of the contribution of the species to the variability of the analyzed traits, one-way analysis of variance was used to iden-

Table 1. Factor loading of behavioral acts demonstrated by rodents of the studied species in the open field test

	Factor 1: physical activity	Factor 2: emotionality
Activity latency	–0.46	–0.16
Vertical activity	0.72*	–0.12
Horizontal activity at the periphery	0.80*	–0.11
Horizontal activity in the center	0.95*	–0.13
Grooming	0.14	0.17
Defecation, acts	0.00	0.96*
Defecation, number of fecal boluses	–0.04	0.95*
Urination	–0.07	0.23
Burrowing activity	0.08	0.00
Bounce	0.21	–0.06
Shaking off	0.04	–0.04
Sipping	–0.05	0.11
Vocalization	–0.06	–0.09
Explained variance, %	19.4	11.2

Behavioral acts that make the greatest contribution to the values of the components are marked with an asterisk (*).

tify the dependences between the studied indicators; Spearman's rank correlation coefficients were used. Calculations were performed using the Statistica package version 12, produced by Statsoft Inc.

The Latin names of the species are given in accordance with the latest summary of Palearctic arvicolines (Kryštufek and Shenbrot, 2022).

RESULTS

Among species under consideration, the maximum life span when kept in captivity was recorded in the northern mole-vole and the flat-headed vole (Table 2). Median life expectancy was highest in Djungarian hamsters. Both indexes were statistically significantly correlated with each other (*Rs* = 0.78; *P* < 0.05). The dynamics of mortality was also significantly (Gehan–Wilcoxon test, *P* < 0.001) differed in different species (Fig. 1). Red-backed, narrow-skulled, and flat-headed voles had higher mortality than other species in the early stages of their life cycle. The northern mole vole and the flat-headed vole demonstrated relatively low mortality at the late stages of ontogeny. The species affiliation had a statistically significant effect on indexes reflecting the state of reproductive (brood size) and somatic (body weight, muscle strength, locomotor activity) functions (Table 2). The size of the litter and emotionality in the open field test negatively correlated with both the maximum and median life span, metabolic rates only with the maximum, and muscle strength only with the median. Locomotor activity was positively correlated with median life expectancy. No statistically significant correlations with life expectancy were found for body weight (Figs. 2–5, Table 3).

DISCUSSION

All the species considered in the work, with the exception of the Djungarian hamster (representative of the subfamily Cricetinae), belong to the same subfamily—voles (Arvicolinae), have partially sympatric ranges, but differ in body weight, preferred biotopes, food specialization, and the spatial and ethological structure of populations, demonstrating wide range of life forms. The analyzed sample includes herbivorous and granivorous, semiaquatic and arid, litter, burrowing, subterranean and petrophilous, and solitary and social species (Bashenina, 1977; Pavlinov and Lisovsky, 2012; Kryštufek and Shenbrot, 2022). It is impossible to consider the entire spectrum of life forms and phyletic lineages of such an extensive family as Cricetidae in one work; however, when choosing species for analysis, we proceeded mainly from the principle of their maximum ecological diversity. A wide gradient in the values of environmental factors that affect the species under consideration is reflected both in the morphological traits and in the ethological and physiological characteristics of animals. All of the indexes we considered (with the exception of emotionality in the open field test) with a high level of statistical significance differed in the species under consideration. A detailed analysis of the variability of these indexes was not included in the objectives of this work, but since species of different ecological specialization were used in the work, it can be assumed that the specifics of the habitat make a significant contribution to it.

The species included in the analyzed sample differed significantly in the main parameters of their life cycles. These differences relate, first of all, to the rates of sexual maturation: in small species with a short life cycle (red-backed and gray voles, steppe lemmings,

Table 2. Life span, fecundity (average litter size), and phenotypic traits in eight rodent species of the Cricetidae family in laboratory conditions. As relative characteristics of physical activity and emotionality, the values of the first and second principal components obtained as a result of factor analysis of the data of open field test are given

	Life expectancy, years		Body weight, g	Brood size, individuals	Metabolic rates, mL/(g h)		Muscle strength, g/g mass	Physical activity	Emotionality
	maximum	median			standard	maximall			
Djungarian hamster	3.6	2.6	31.3 ± 1.3	4.4 ± 0.1	3.9 ± 0.3	17.4 ± 0.5	5.2 ± 0.4	0.35 ± 0.08	–0.22 ± 0.10
Northern mole-vole	6.4	2.2	45.8 ± 1.5	2.9 ± 0.1	2.7 ± 0.2	7.7 ± 0.4	5.9 ± 0.4		
Water vole	3.4	1.5	164.7 ± 9.1	4.5 ± 0.4			10.6 ± 0.2	–0.93 ± 0.15	0.33 ± 0.27
Steppe lemming	2.7	1.5	17.9 ± 0.3	3.6 ± 0.2	4.5 ± 0.2	14.3 ± 06	8.1 ± 0.2	0.70 ± 0.08	–0.02 ± 0.12
Narrow-skulled vole	2.7	1.3	20.0 ± 0.9	6.2 ± 0.4	4.0 ± 0.1	15.6 ± 0.6	10.0 ± 0.5	–0.35 ± 0.08	0.05 ± 0.9
Red-backed vole	2.7	0.8	21.9 ± 0.7	6.4 ± 0.5	4.0 ± 0.1	15.9 ± 0.3	9.1 ± 0.3	–0.55 ± 0.08	0.13 ± 0.09
Tuvan vole	4.2	2.7	43.2 ± 2.1	2.6 ± 0.2	2.9 ± 0.2	11.1 ± 0.5	7.1 ± 0.6	1.48 ± 0.11	–0.57 ± 0.05
Flat-headed vole	6.3	1.7	42.9 ± 2.4	3.3 ± 0.3	2.4 ± 0.2	11.0 ± 0.4	8.5 ± 0.6	0.75 ± 0.25	–0.60 ± 0.06
Fisher criterion values				33.2	16.0	16.6	18.2	38.3	2.3
Significance level, *P*				0.001	0.001	0.001	0.001	0.001	0.05

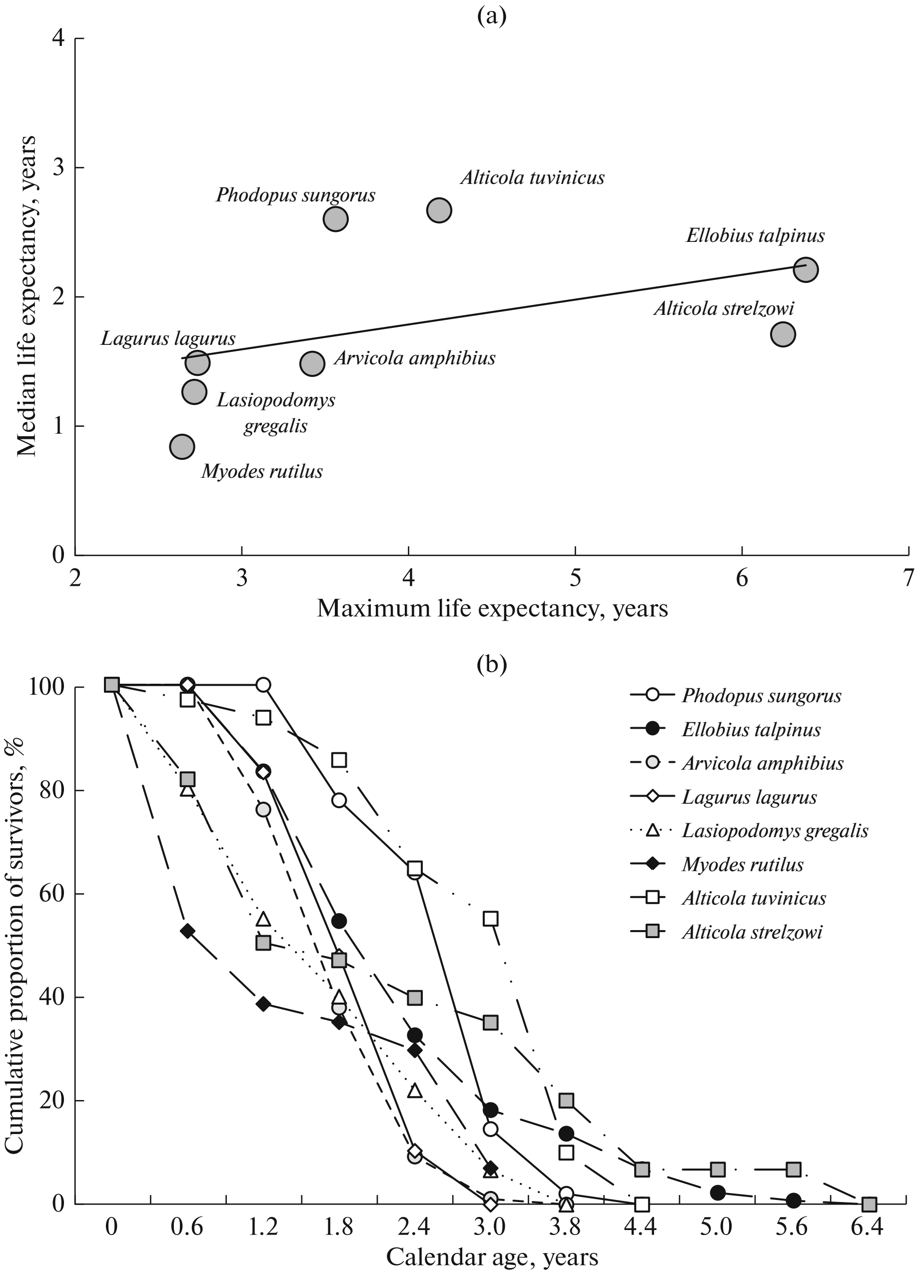

Fig. 1. Survival rate of eight species of murid rodents in laboratory conditions: (a) the relationship between the maximum and median life expectancy, (b) age-relared dynamics of mortality.

and dwarf hamsters), puberty can occur at the age of 1.5–2 months, while in rock voles, only in the second year of life (Bashenina, 1977; Pokrovsky and Bolshakov, 1979). In water voles and mole-voles, also mostly overwintered individuals breed (Evdokimov, 2001; Panteleev, 2001). The correlation between the rate of puberty and life span is clearly manifested both at the intra- (Shvarts et al., 1964) and at the interspecies levels. In addition to the rate of sexual maturation, one of the main predictors of life span at the species level is body weight (Magalhaes et al., 2007). From the point of view of mechanistic ideas about aging, the long life span of large animals may be due to the inverse relationship between body weight and the specific (per unit body mass) value of energy exchange (Pearl, 1928; Kleiber, 1932), from the point of view of evolutionary theory, a low risk of non-age-related death, which in rodents is largely determined by the probability of predation (Gorbunova et al., 2008). However, in the eight representatives of the Cricetidae family that we examined, body weight did not correlate with either the maximum or median life expectancy. The absence of

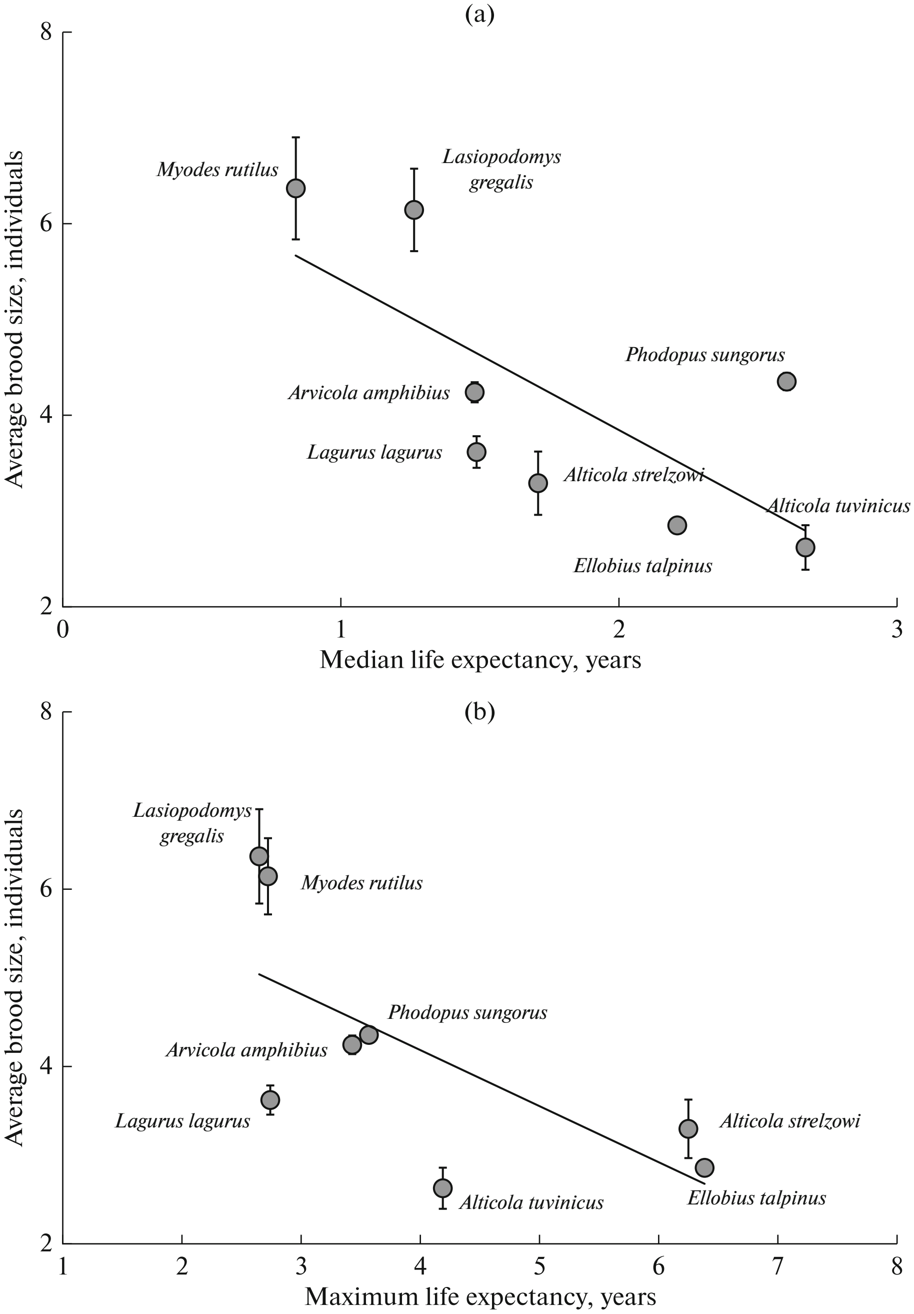

Fig. 2. The relationship between mean brood size and median (a) and maximum (b) life expectancy.

statistically significant correlations (although in the presence of a positive trend) can be associated both with a small sample size and with the specifics of the formation of idioadaptations, in which body weight has a significant thermoregulatory significance. It is well known that, in rodents, the evolutionary tendency to increase in size is characteristic of solitary (compared to colonial forms), subterranean (McNab, 1979; Dammann and Burda, 2007) and semiaquatic (Panteleev, 2001) species. In both cases, the increase in size does not obviously lead to a decrease in the risk of predation. The exclusion of the water vole from the analyzed sample makes statistically significant ($R = 0.82$; $P < 0.05$) the correlation of body weight with maximum (but not median!) life expectancy.

The concept of competition for resources between somatic and generative functions is one of the cornerstones in modern evolutionary biology (Kirkwood, 1977; Stearns, 1992). In particular, for mammals, there is a clear evolutionary trend toward earlier breeding dates and increased fecundity in species with a high mortality rate (Promislow and Harvey, 1990). In

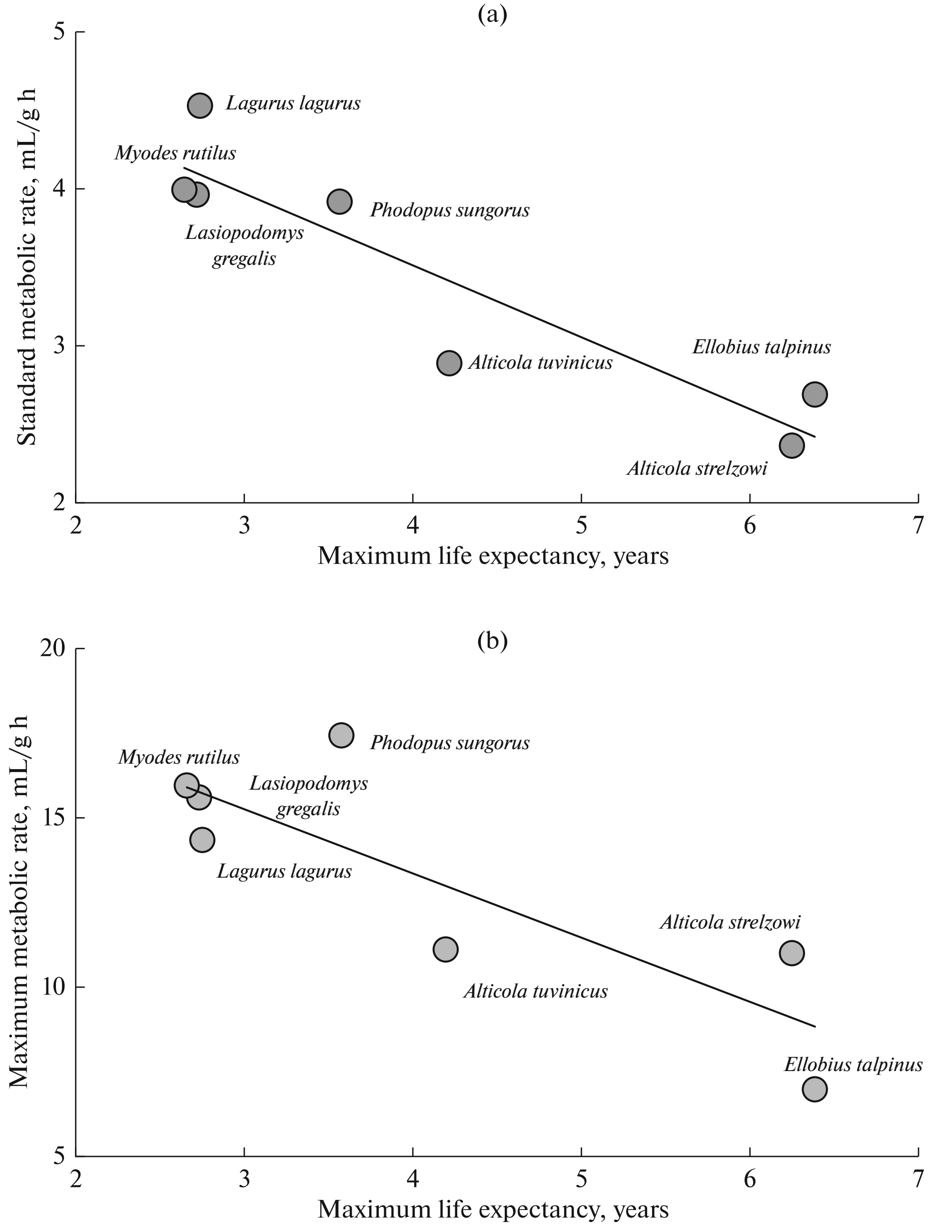

Fig. 3. The relationship between the standard (a) and maximum (b) metabolic rate and maximum lifespan.

the eight studied species of cricetids, we found a negative relationship between both considered life expectancy indicators and the current costs of reproduction, as was previously shown for bats (Wilkinson and South, 2002). The experimental protocol we used did not allow us to reliably determine the timing of

Table 3. The values of the coefficients of rank correlation between life expectancy and phenotypic traits in eight species of rodents of the Cricetidae family

	Body weight, g	Brood size, individuals	Energy exchange, mL/(g h)		Muscle strength, g	Physical activity	Emotional reality
			standard	maximum			
Maximum life span	0.64	**–0.83***	**–0.86***	**–0.79***	–0.57	0.68	**–0.79***
Median life expectancy	0.38	**–0.76***	–0.57	–0.29	**–0.81***	**0.79***	**–0.79***

* Values are valid ($P < 0.05$).

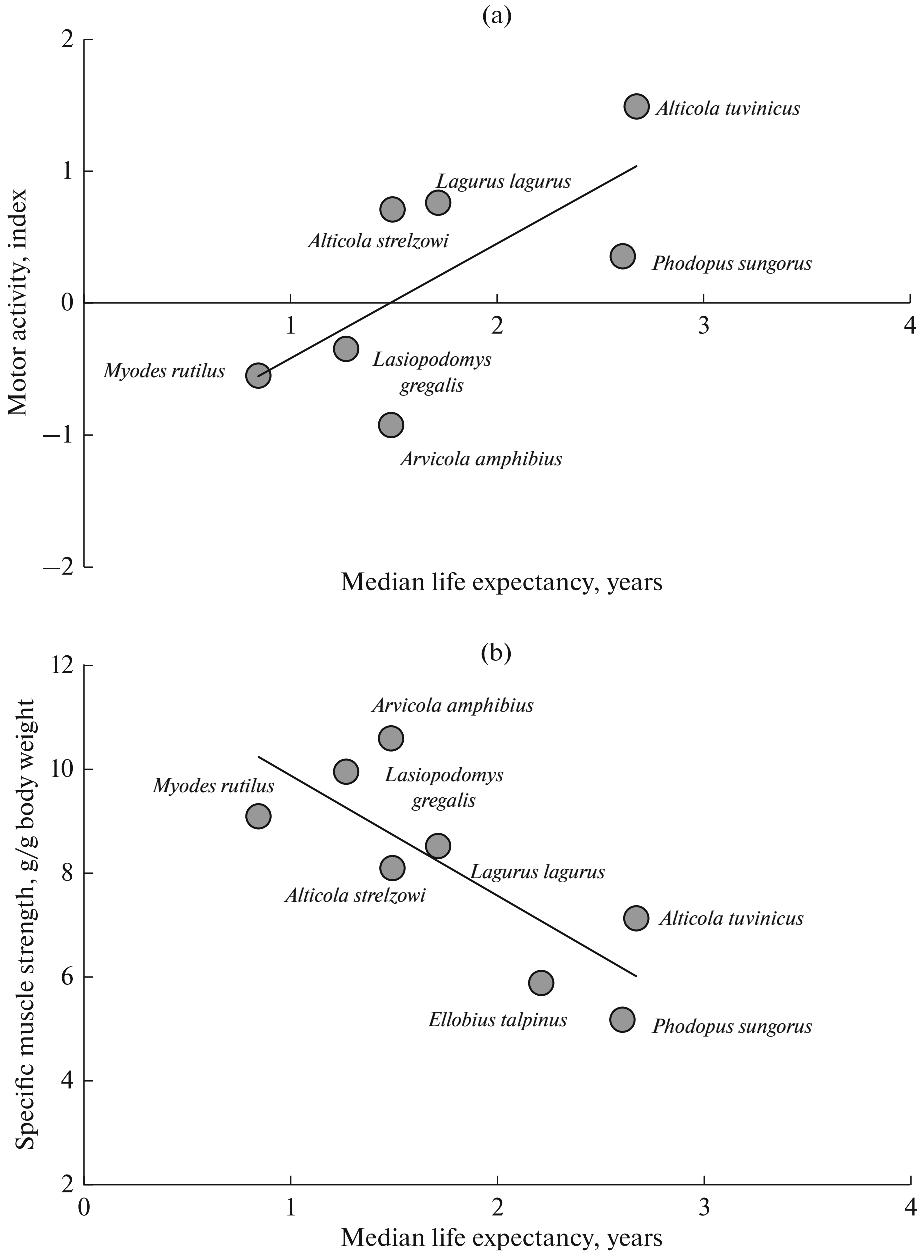

Fig. 4. The relationship between locomotor activity in the open field test (a) and mass-related muscle strength (b) and median life expectancy.

puberty; however, it should be noted that long-lived species-the common mole vole and rock voles-in nature start breeding, as a rule, only in the second year of life (Pokrovsky and Bolshakov, 1979; Evdokimov, 2001).

A fairly large number of works have been devoted to the analysis of the relationship between life expectancy and the intensity of basal metabolic rate. The presence of such a dependence is the starting point for mechanistic theories of aging (Speakman et al., 2002). From the point of view of evolutionary theory, its possible explanation may be related to the presence of an allometric relationship between body size and relative (per unit body mass) intensity of energy exchange (Darveau et al., 2002). Larger animals have a smaller mass-related metabolic rates compared to small ones and at the same time are better protected from predators. In our case, an additional contribution to the observed regularity is made by the presence in the studied sample of subterranean and mountain species subjected to chronic hypoxia and having the minimum value of basal metabolic rates in the considered sample (McNab, 1979; Ar, 1987). Hypoxia, both acute and chronic, is obviously one of the significant factors in

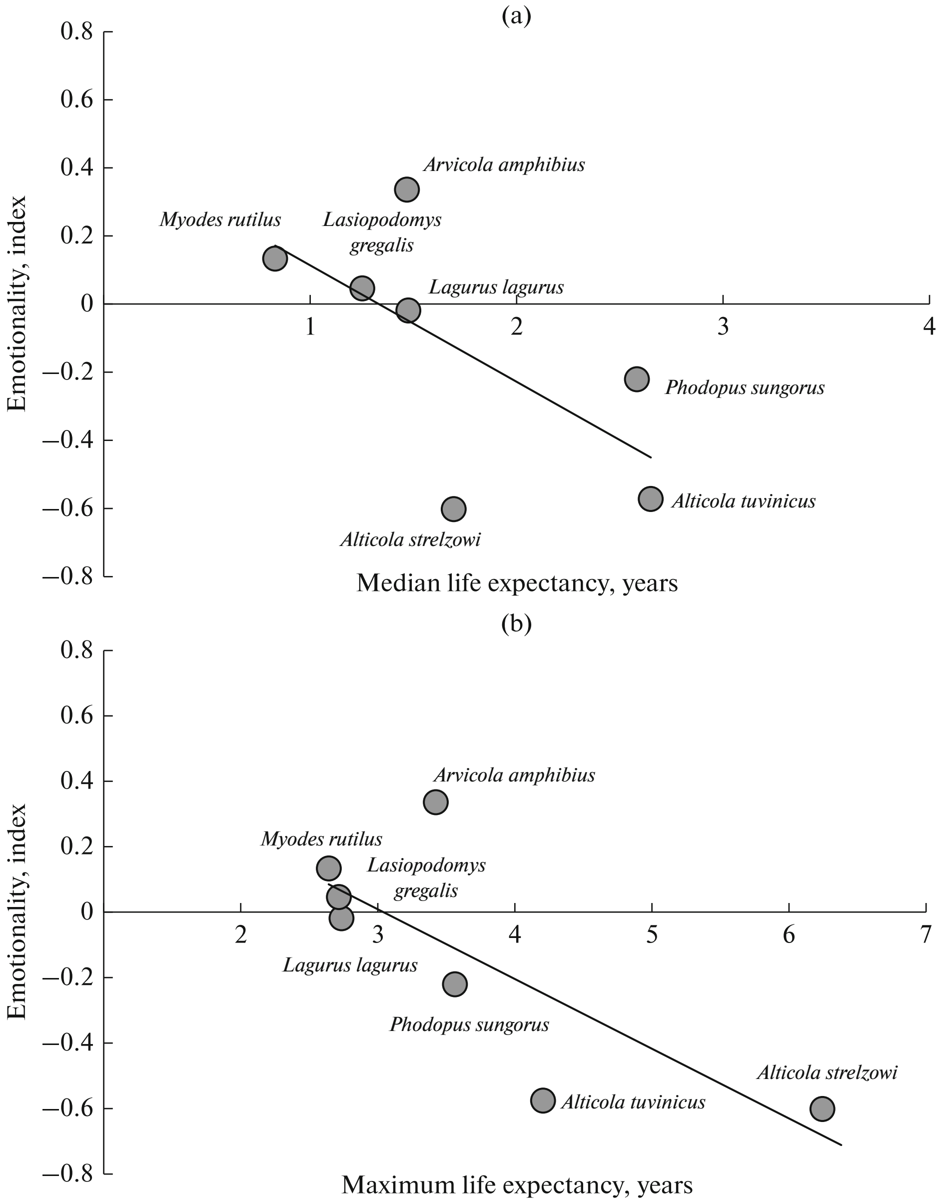

Fig. 5. The relationship between emotionality and median (a) and maximum (b) life expectancy.

increasing life expectancy (Agadzhanyan et al., 1995). The water vole, as a diving species periodically subjected to acute hypoxia (Hochachka et al., 1999; Panteleev, 2001), is a very interesting object for comparative analysis; however, we had to exclude it from consideration because of its incomparable size with other species. In addition to the gas composition of the atmosphere, the intensity of metabolism is also significantly affected by environmental factors such as geographic latitude, climatic conditions, calorie content, and food availability (Lovegrove, 2000, 2003). Since in nature the real energy consumption by animals (especially endothermic ones), as a rule, significantly exceeds the level of basal metabolic rate, it is proposed to consider average daily energy consumption as a more adequate characteristic for the analysis of allometric dependences with life span (Speakman et al., 2002). However, owing to technical difficulties, this approach is still not widely used in comparative studies. Therefore, as a characteristic of the species-specific level of energy consumption that animals face in nature, we used the value of the maximum metabolic rate. We used this indicator, measured under conditions of acute cooling or physical exertion, to assess the adaptive capabilities of the body, allowing it to adequately respond to environmental challenges (Hayes, 1989; Moshkin et al., 2002; Rezende et al., 2004; Polikarpov et al., 2016); however, there are no data on its correlation with species-specific or individual indexes of life expectancy in the literature. The presence of a negative relationship, revealed in our work, can be of the same nature as for the basal metabolic rate and be interpreted from both mechanistic and evolutionary positions. A sharp activation of energy exchange up to maximum level in stressful situations, inevitable in nature (uncomfortable temperatures, predator attacks), with a corresponding peak load on the circulatory, nervous, and endocrine systems, can lead to rapid deterioration of the body. The frequency of such loads is inversely proportional to the stability of the environmental conditions and its protective properties.

Metabolic limitations may be partly related to the variability in such indexes as muscle strength and locomotor activity in the open field test. However, in addition to the size of the body, the specifics of the habitat conditions and life history of the species can play an important role here. Both indicators correlate (in different directions) with the median, but not with the maximum life expectancy. Muscle strength, as well as other indicators related to energy exchange-body weight and locomotor activity-can be determined by the possibilities of resource provision of the body; however, it is obvious that, with the experimental approach we use, it also depends on the design of the locomotor apparatus and the nature of the biomechanical loads on it (Gambaryan, 1972). The water vole demonstrated the maximum values of this indexes among the considered species. The load on the forelimbs in this species can be associated both with swimming in summer and with intense burrowing activity in winter. Significantly lower strength of the forelimbs relative to body weight was demonstrated by species of open spaces and an underground species-the northern mole-vole, which mainly uses incisors for digging. At the species level, muscle strength is considered one of the most reliable predictors of residual life span (Rantanen et al., 2000; Leong et al., 2015). The lack of correlation between the muscular strength of the forelimbs and the maximum life span of the species is obviously due to the ambiguity of the evolutionary tendencies that determine it.

No less wide is the range of factors affecting the locomotor activity of animals, including those of its components that appear when animals are tested in the open field test. In addition to spontaneous motor activity, such components can be exploratory activity, a desire to leave an uncomfortable environment, etc. (Walsh and Cummim, 1976). A decrease in locomotor activity, in turn, is considered as one of the main manifestations of the so-called sick-syndrome that develops in the body when toxins or infectious agents enter (Dantzer, 2001). A huge amount of work has been devoted to the influence of physical activity on human longevity (Powell et al., 1987), but there are surprisingly few data on the relationship between these indexes in vertebrates (Ingram et al., 2000). In studies performed on the social subterranean species of Bathyergidae family, the Ansell's mole—rat (*Fukomys anselli*), it was not possible to reveal differences in the activity budget between breeding and non-breeding individuals (Schielke et al., 2012), despite almost two-fold differences in median and maximum life span (Dammann and Burda, 2007). The correlation of this indexes with the median- and its absence with the maximum species life expectancy revealed in our work, indicate a direct functional relationship between the physical state of the individual and the time of its survival. This makes it possible to use the level of spontaneous locomotor activity to assess the quality of life of both individuals and animal species when kept in laboratory conditions.

One of the main individual characteristics considered when testing animals in an open field is emotionality, the manifestation of which, first of all, such behavioral acts as grooming, defecation, and urination are considered (Hall, 1934, 1936). When analyzing the variability of the behavioral repertoire in a sample formed from seven species of rodents of the Cricetidae family, 11.2% of the explained variance was taken by the second principal component, formed mainly by the frequency of defecation acts and the number of boluses. A less significant contribution to this component was made by the frequencies of grooming and urination (Table 1). Despite the ambiguity of the biological interpretation of the concept of emotionality (Izard, 2010; Paul and Mendl, 2018), the results of testing in an open field, including those in the study of wild rodent species (Zadubrovsky et al., 2017, 2021), are well interpreted from the standpoint of individual and specific features of behavior in light of the concept of a behavioral syndrome (Réale et al., 2010). The negative correlation of the emotionality index demonstrated in the open field test with the median life span of the species considered here reflects the well-known fact of the influence of the mental state of the body on its physical health. Under unfavorable conditions, an increased emotional background can become a prerequisite for the development of a state of chronic stress, which has a depressing effect on all aspects of the organism's functioning (Selye, 1979). The cumulative consequences of stresses acting on an individual during life are considered as one of the mechanisms of aging (Dilman, 1986). On the other hand, the behavioral response to an unfamiliar environment is considered to be an important component of the "personality" of an individual, affecting the complex of life-history, behavioral, and physiological parameters that determine the position of an individual (and species) in the "pace of life" continuum (Ricklefs and Wikelski, 2002; Réale et al., 2010). "Short-lived" species with a high intensity of metabolic processes, exposed to the high risk of predation, reacted more emotionally to the experimental conditions. It should also be emphasized that, in the absence of the mole-voles in the sample, which were excluded from the analysis because of the low frequency of behavioral acts interpreted as manifestations of emotionality, long-lived species were represented only by rock voles living in nature in the three-dimensional space of stone placers. It is possible that the test conditions were less stressful for them than for other species (Zadubrovsky et al., 2017).

The comparative analysis of the adaptive strategies of rodent species of various ecological specializations carried out here indicates a close relationship between the species-specific features of physiology and behavior, on one hand, and life expectancy, on the other hand. With the exception of body weight, which is considered as one of the main evolutionary determinants of longevity at the level of large taxa (Magalhaes et al., 2007), all indicators considered in this work correlated with the maximum and/or median life span of the species. In most cases, the observed correlations can be interpreted both from the standpoint of evolutionary ideas and from the standpoint of mechanistic ideas about aging. It should be noted that there is no conceptual antagonism between the two considered groups of hypotheses. According to the evolutionary theory of aging, the role of natural selection is to achieve the optimal allocation of resources for reproduction and somatic demands, including a number of reparative functions that ensure the restoration of damage that occurs during life (DNA breaks, oxidative damage, dysfunction of membranes and long-lived proteins, etc.). Thus, both at the organismal and at the species level, life span is determined by the balance of the resource provision of these two processes (Kirkwood, 1977; Kirkwood and Rose, 1991). However, it is the maximum species values (if their assessment is correct) that reflect the evolutionary component of the species life span. The median life expectancy, quite obviously, is a characteristic of a particular sample and depends on the extent to which animals manage to realize their evolutionary potential in specific conditions of keeping (Morrison et al., 1977). Relatively high mortality in the early stages of ontogeny can be both part of an adaptive strategy (Stearns, 1992) and a reflection of the ability of individuals of this species to adapt to the conditions of their keeping. In addition to the temperature regime, adequate feeding, the anxiety factor, and other factors affecting the survival of animals in captivity, for example, for social underground species, the impossibility of implementing reproductive motivation, can become a significant factor in reducing individual life expectancy (Dammann and Burda, 2007; Novikov et al., 2015a, 2015c), and for high-mountainous species, the partial pressure of gases in the inhaled air is not quite comfortable (Novikov et al., 2022).

The eight species of rodents considered in our work are far from exhausting the diversity of life forms of representatives of the Cricetidae family, which is unique in species richnes and ecological diversity. Among other things, the phylogenetic history of the taxon can make a significant contribution to the interspecies variability of the parameters under consideration (Harvey, 1996). The lack of reliable data did not allow us to take into account the phylogenetic relationships of species in our work; however, in all cases, with the exception of rock voles, each genus was represented by one species, which made it possible to partially neutralize the influence of the phylogenetic signal. It should also be emphasized that the phylogenetically closest clades are rock and red-backed voles (Kryštufek and Shenbrot, 2022), and they differed significantly in the values of most of the considered indicators.

The attempt made here to compare the complex of functional characteristics in ecologically contrasting species will make it possible to understand how severe the evolutionary constrains on increasing the maximum lifespan are, and what indicators of the state of the body most significantly affect the median lifespan in laboratory conditions. The variability of the ratio between the maximum and median lifespan can serve as the basis for the development of new criteria for the wellfare of species kept and bred for various purposes under the control of humans, and the search for ways to increase their survival may also be useful for practical gerontology.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement of the welfare of animals. Conditions were adapted to the biology of each species to minimize the harmful and stressful effects of cage keeping. The climatic regimes in the laboratory rooms were comfortable for the animals; the usual diet was balanced and included all the nutrients necessary for normal growth and development. The premises were periodically sterilized with a quartz lamp. We did not disturb the animals without reason. In the event of death, the individuals were carefully removed from the cages. The experimental protocol was brought into accordance with the rules for conducting scientific research using experimental animals, approved by the order of the Presidium of the USSR Academy of Sciences of April 2, 1980, no. 12000-496 and the order of the Ministry of Higher Education of the USSR of September 13, 1984, no. 22. The experimental protocol was approved at a meeting of the bioethics committee of the Institute of Systematics and Ecology of Animals of the Siberian Branch of the Russian Academy of Sciences.

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