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RESEARCH ARTICLE

On the Concentration of Vitamins A and E in the Tissues of the Bank Vole (*Myodes* (*Clethrionomys*) *glareolus*) and Common Shrew (*Sorex araneus*) Inhabiting Karelia

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Abstract—We have studied the concentration of vitamins A (retinol) and E (α-tocopherol) in the tissues of the bank vole (*Myodes* (*Clethrionomys*) *glareolus*) and common shrew (*Sorex araneus*) inhabiting the northern periphery of its natural habitat. The distribution of vitamin A in the common shrew and bank vole tissues is similar: the highest concentration is found in the liver, and the lowest level is found in the heart. Age-related differences in the retinol concentration are detected in the kidneys of the two species, as well as in the skeletal muscle of the shrew. A significantly lower vitamin E concentration is found in all organs of young shrews before wintering, compared to adult overwintered animals, while in the bank vole no such age-related differences are found. Interspecies differences in the levels of vitamins A and E in the liver of overwintered animals are revealed. The results obtained show that the concentration of vitamins A and E in the tissues of the bank vole and the common shrew is determined by metabolic processes and the ecological characteristics of the species. The level of vitamins in the common shrew depends largely on age.

Keywords: vitamin A, vitamin E, metabolism, age, season, mammals

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INTRODUCTION

The habitat of mammals in subarctic regions is subject to profound seasonal changes. To successfully survive in cold climates, animals have developed a variety of physiological adaptations aimed at conserving energy and increasing resistance to cold. At the same time, not only winter can be a difficult period for small mammals, which face extremely high energy needs during the reproductive season in spring and summer [1, 2].

Differences between species of small mammals are especially evident in habitats with high seasonality and are determined by the behavioral, anatomical, and physiological characteristics of animals [3]. The bank vole (*Myodes* (*Clethrionomys*) *glareolus* Schreber, 1780) and common shrew (*Sorex araneus* Linnaeus, 1758) are common species in the forest communities of Karelia. A common ecological feature of the two species belonging to different taxa is their habitat in a narrowed annual range of external temperatures. Both species have developed adaptations to survive during winter with low ambient temperatures: they do not hibernate and are active during the cold season. At the same time, rodents and shrews are two taxa with completely different evolutionary histories. Small insectivores and rodents exhibit significant differences in diet, metabolic rates, reproductive strategies, and others. It is assumed that reproduction, delayed in shrews in Karelia until the second calendar year of life, is the result of selection for traits that ensure successful survival during winter, which is a period that is more difficult for shrews than for rodents. In rodents, in contrast, opportunistic reproduction is the most prominent characteristic that helps increase reproductive output and is a major strategy in evolution that arose as a response to increased predation [1, 3, 4]. Under pessimal conditions, with an increase in overall mortality, the importance of juvenile reproduction for preservation of the population increases [5, 6].

Studying the mechanisms of the stability of small mammal populations includes the study of physiological systems that directly or indirectly respond to environmental changes [7]. One of the main factors determining the pace of individual development and life expectancy is the metabolic rate, which is very high in small short-lived species. Small mammals use a set of morphological and physiological adaptations that ensure a continuous supply of oxygen to tissues to maintain oxidative metabolism [8, 9]. A high level of aerobic metabolism affects the rate of accumulation of metabolic products formed in free-radical oxidation reactions and other processes, therefore, among the seasonal adaptations of nonhibernating small mammals, changes in the state of the antioxidant system may be of significant interest.

Vitamins A and E play an important role in metabolism, are characterized by versatile physiological and biochemical effects, and are low-molecular-weight antioxidants. Vitamin A is of particular importance in the process of light perception, is necessary for normal fetal development, and also affects the process of an increase in white and brown adipose tissue, which is important for the successful wintering of mammals [10, 11]. Vitamin E in the body plays the role of the main biological antioxidant and is a regulator of energy metabolism [12]. Vitamin E has a pronounced synergy with vitamin A and protects it from oxidation.

The purpose of the work is to study the concentration of fat-soluble vitamins A and E in organs and tissues of bank voles and common shrews of different ages. The concentration of vitamins A and E in the tissues of these species has not been previously assessed.

MATERIALS AND METHODS

The objects of the study were the bank vole (*Myodes* (*Clethrionomys*) *glareolus* Schreber, 1780) ($n = 62$) and common shrew (*Sorex araneus* Linnaeus, 1758) ($n = 38$), which were obtained in natural conditions in the Republic of Karelia (61°–63° N, 30°–36° E). The work of catching the animals was carried out at the expedition base of the Institute of Biology of the Karelian Research Center, Russian Academy of Sciences (Republic of Karelia, Pryazhinsky district, Kaskesnavolok village) from 2016 to 2022. In the spring, animals were caught from the end of April and during May; in the summer–autumn period, from the end of July until November. Permits for catching the animals were issued by the Hunting Department of the Ministry of Agriculture, Fishing and Hunting of the Republic of Karelia. The animals were caught using standard methods [13] in the main types of biotopes, using standard factory-made traps (presses) and trapping ditches. Traps were installed in lines of 25 pieces with an interval of 5 m. Each line worked for 3 days, with a single check every day. Trapping ditches 30-m long with three trapping cylinders, 1/3 filled with water, were checked once a day. Each groove worked for 5 days. After capture, the animals were weighed, their age and sex were determined, and tissue samples were collected and frozen until analysis. To determine the age of bank voles, a method developed by N.V. Tupikova et al. was used [14], which makes it possible to determine the age of the animal with an accuracy of up to two months based on the degree of tooth development. When assigning an animal to a particular age group, other signs were additionally taken into account: the development of the thymus, the structure of the skull, the state of the reproductive system, etc. When dividing the animals into generations, a functional-ontogenetic approach was used, which was applied and described by E.V. Ivanter [6, 15] and G.V. Olenev [16, 17]. In shrews, the shape (configuration, condition of the sutures) of the skull and the degree of tooth wear were used as the main age criteria, and the wear patterns of the hair on the tail, paws, and ears were used as auxiliary criteria [15]. In doubtful cases, other indicators were also used, in particular, the size of the thymus, which completely involutes by the autumn of the first year of life and is practically not expressed in overwintered animals.

The concentration of vitamins A (retinol) and E (α-tocopherol) was determined in the liver, kidneys, heart, and skeletal muscle using high-performance liquid chromatography [18]. Tissue samples (100 mg) were homogenized in 0.9 mL of 0.25-M sucrose solution (pH 7.4) as a suspension medium. A 0.025% solution of butylated hydroxytoluene in ethyl alcohol was added to the homogenate and mixed thoroughly to precipitate the proteins. A 0.0125% solution of butylated hydroxytoluene in n-hexane was added, the mixture was shaken for 5 minutes, then centrifuged at 3000 *g* for 10 min and kept for 40 min at 4°C. The sample for chromatographic analysis was taken from the upper hexane layer; the eluent was a mixture of hexane and isopropanol in a ratio of 98.5 : 1.5. Detection was carried out at 292 nm for α-tocopherol and 324 nm for retinol. When constructing the calibration curves, standard solutions of retinol and α-tocopherol (Sigma-Aldrich, United States) were used.

The obtained data were processed using MS Excel 2007 and Statgraphics 5.0 software packages. For statistical analysis, the Kruskal–Wallis test was applied, followed by pairwise comparisons using the Mann–Whitney U test, and correction for multiple comparisons was used. The data in the graphs are presented in the form of the median and interquartile range. Differences were considered statistically significant at $p < 0.05$. No significant sex differences were found in the studied parameters, and therefore data for males and females were analyzed together.

The research was carried out using scientific equipment of the Center for Collective Use of the Federal Research Center “Karelian Scientific Center, Russian Academy of Sciences.”

RESULTS

The highest concentration of vitamin A was found in the liver of animals of both species (Fig. 1). The level of retinol in the kidneys of bank voles of late generations was significantly lower compared to animals of early generations and overwintered individuals. In overwintered shrews, a higher vitamin concentration was found in the kidneys and skeletal muscle than in young animals. In the liver of overwintered bank voles, the vitamin A concentration was significantly higher than in adult overwintered shrews.

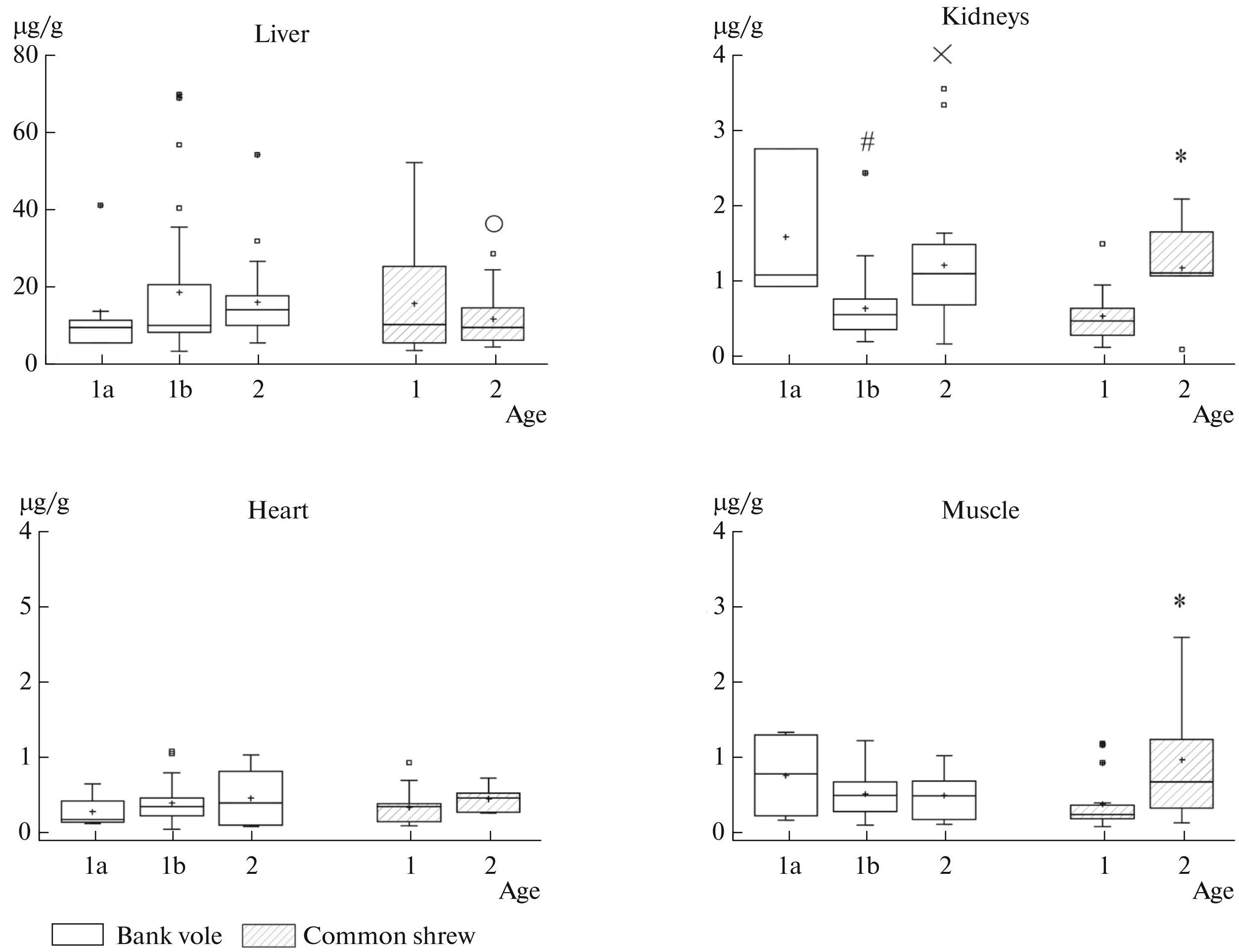

Fig. 1. Vitamin A concentration in the organs of bank voles and common shrews. Designations: (+) is the average, (–) is the median, □ is 25–75%, ⌶ is the statistical range, ° is drop-down options; 1 is underyearlings, 1a is underyearlings of early generations, 1b is underyearlings of late generation, and 2 is overwintered animals. The differences are significant compared to: * is underyearlings, ○ is overwintered voles, # is underyearlings of early generations, × is underyearlings of later generations ($p < 0.05$, Kruskal–Wallis criterion with post-hoc test according to Mann—Whitney U test).

In the bank vole, no significant age-related differences in the concentration of vitamin E in tissues were found (Fig. 2). In young shrews, the level of vitamin E in all tissues was significantly lower than in adult animals. At the same time, in the heart, whose energy metabolism is very high, the level of vitamin E in shrew underyearlings was significantly lower compared to both adults and bank-vole underyearlings. The concentration of vitamin E in the liver of overwintered shrews was significantly higher than that of the vole.

For control of the physiological state, the body weight of the animals was determined. In the bank vole, the average weight of overwintered animals and underyearlings did not differ significantly (Fig. 3). At the same time, underyearlings of later generations of voles had a lower body weight compared to early generations and adult overwintered animals. Juvenile shrews caught in the autumn months had a lower body weight than adult overwintered animals.

DISCUSSION

The results of the study showed that the concentration of vitamins A and E in the tissues of the bank vole and the common shrew has high variability due to significant differences in the physiological state of animals living in the wild, as well as a number of factors: the biological function of the organs, the taxonomic affiliation of the animals, the level and type nutrition, age, participation in reproduction, etc. The level of retinol and tocopherol in the studied species is generally low compared to larger representatives of the orders Rodentia and Eulipotyphla [19].

The concentration of vitamins A and E depends on the type of tissue, and in most mammals the highest levels of vitamins are found in the liver, from where

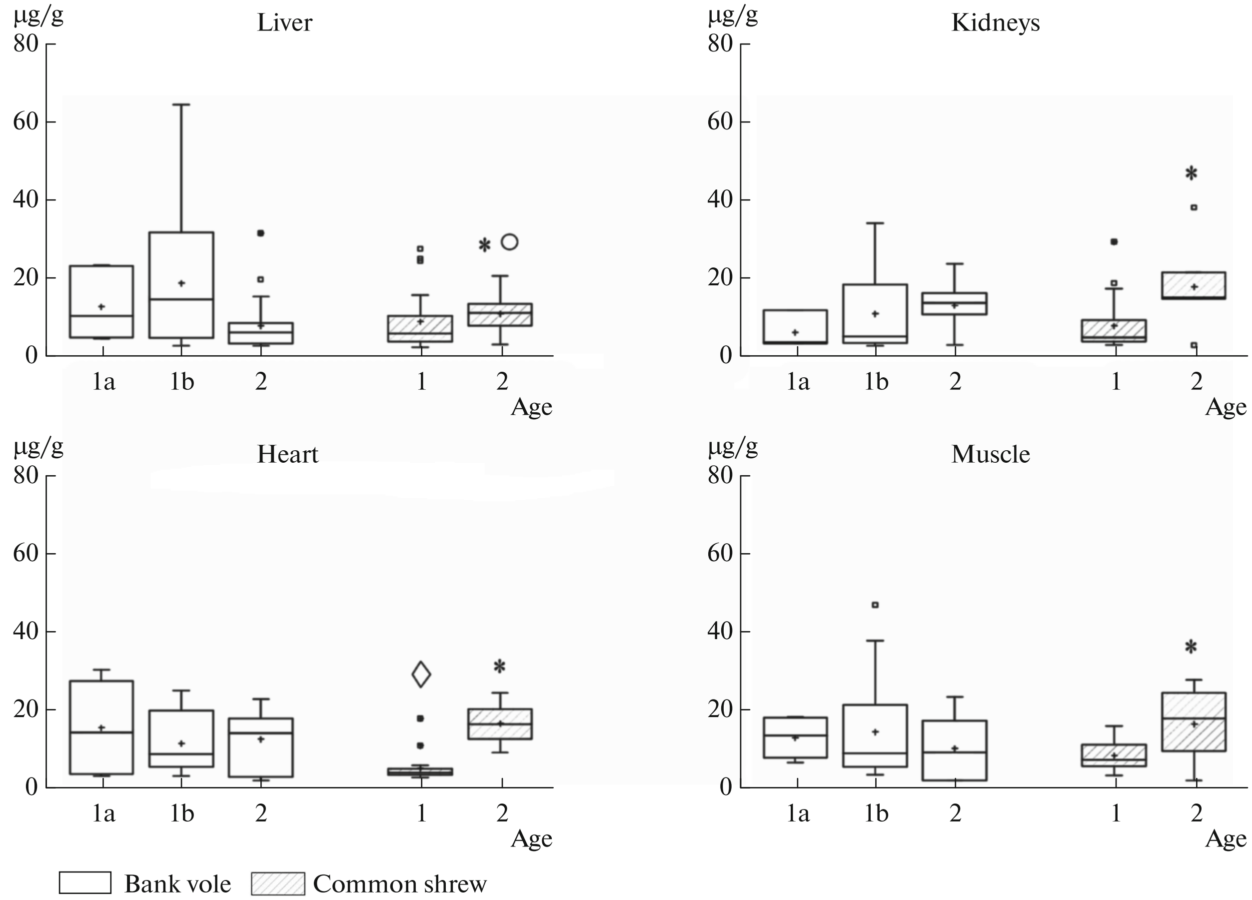

Fig. 2. Vitamin E concentration in the organs of bank voles and common shrews. Designations: (+) is the average, (–) is the median, □ is 25–75%, ⌶ is the statistical range, ° is drop-down options; 1 is underyearlings, 1a is underyearlings of early generations, 1b is underyearlings of late generation, and 2 is overwintered animals. The differences are significant compared to: * is underyearlings, ◇ is underyearling voles, ○ is overwintered voles ($p < 0.05$, Kruskal–Wallis criterion with post-hoc test according to Mann–Whitney U test).

they are transported to other organs. In our study, higher levels of vitamin A in bank voles and common shrews were also found in the liver; retinol levels were significantly lower in the kidneys, cardiac, and skeletal muscles. In bank voles of later generations, the retinol concentration in the kidneys was lower than in the spring–summer generation of animals. Rodents of different seasonal generations are distinguished by a whole complex of morphophysiological characteristics: animals born in summer–autumn have a low growth and development rate, lower body weight and nutritional state compared to voles of early generations [20]. The identified differences are probably not associated with changes in the overall level of vitamin A in the body, since no differences were found between animals of different generations in the liver, which stores and regulates its metabolism. The kidneys are the site of the formation and removal of the end products of vitamin A metabolism, an excess of which is toxic to the body. The lower retinol concentration in animals born in summer–autumn is probably due to a decrease in the excretory function of the organ in the pre-winter period. It should be noted that the level of vitamin A in the kidneys of late-generation vole underyearlings was also lower compared to overwintered animals. A similar difference was observed in the kidneys and skeletal muscle of the common shrew. It is known that small mammals are characterized by an autumn decrease in body weight and some major organs, which contributes to successful overwintering [1–3, 6, 20, 21]. Moreover, in shrews these changes are more pronounced than in rodents [2, 7, 20, 22, 23]. In spring, the reverse process occurs: body weight and internal organs increase, accompanied by the accumulation of nutrients, which is aimed at preparing for reproduction, which requires large energy expenditures [2, 6]. The retinol levels in the kidneys and skeletal muscle are significantly lower than in the liver, but these tissues are also storage sites for micronutrients. In other small mammal species, the vitamin A concentration has been studied mainly in the liver. It was found that in the root vole its lowest level was observed in young individuals in winter [24]. In red and water voles, muskrats, and chipmunks, the vitamin A concentration of underyearlings was lower compared to adult animals [25].

The total level of vitamin A in the liver is proportional to the amount obtained from food, but this relationship is not linear. When vitamin A intake is low, storage in the liver is low, since most of the vitamin entering the body is used to perform its biological functions. In our study of overwintered animals, a lower retinol concentration in the liver was found in the shrew compared to the bank vole. The discovered differences may be associated both with food specialization and with different levels and characteristics of metabolic processes in voles and shrews. It has been found that retinoic acid, the biologically active form of vitamin A, takes part in the regulation of energy metabolism, facilitating the acquisition by white adipocytes of properties characteristic of brown adipose tissue [26]. Finnish researchers believe that lipid metabolism is more important for shrews than for voles. In overwintered shrews significant reserves of adipose tissue were found, represented predominantly by brown fat, which is assumed to play the role of white fat in *Sorex araneus* [21, 27]. In winter, this species exhibits the highest metabolic activity of brown adipose tissue, which is aimed at maintaining thermogenesis [28].

The liver is an important storage site for vitamin E, where it is incorporated into lipoproteins, in combination with which tocopherol is delivered by the blood to other organs and tissues. Overwintering mouse-like rodents experience a decrease in body weight, which then increases with the onset of spring growth to ensure animal reproduction and normal pregnancy and lactation. However, the seasonal physiological changes occurring in animals did not lead to significant changes in the level of vitamin E in the tissues of bank voles. At the same time, overwintered individuals of the common shrew had a higher level of α-tocopherol compared to underyearlings. It is known that the metabolism of vitamin E in the body is closely related to lipid metabolism. Compared to the bank vole, the common shrew shows more seasonal changes in the amount of brown adipose tissue [29]. In shrews, the rate of fat metabolism is negatively correlated with body size [28]. Probably, in the spring, in overwintered individuals whose body weight was higher than that of underyearlings, a slowdown in fat metabolism processes contributes to an increase in the level of α-tocopherol in the body, despite the fact that this phenotype is characterized by the highest energy consumption [2]. Differences in the concentration of α-tocopherol found in cardiac and skeletal muscles between underyearlings and wintered shrews may also reflect age-related changes in the muscles of shrews [30]. The increase in total vitamin E with aging may represent an adaptive response related to the availability of tocopherol to prevent oxidative tissue damage that increases with age [31].

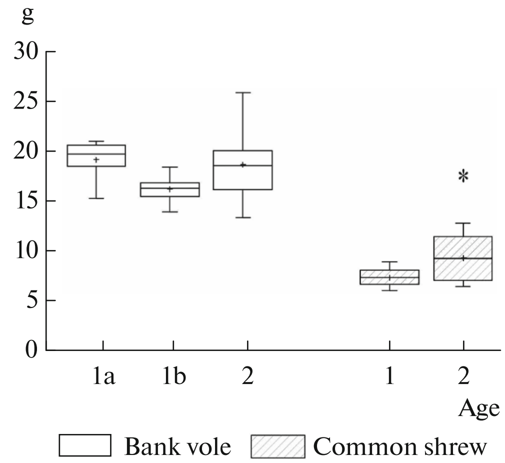

Fig. 3. Bodyweight of bank voles and common shrews. Designations: (+) is the average, (–) is the median, □ is 25–75%, ⌶ is the statistical range, ° is drop-down options; 1 is underyearlings, 1a is underyearlings of early generations, 1b is underyearlings of late generation, and 2 is overwintered animals; * is differences are significant compared to underyearlings ($p < 0.05$, Kruskal–Wallis criterion with post-hoc test according to Mann–Whitney U test).

The concentration of α-tocopherol in the liver of overwintered shrews was significantly higher than that of overwintered voles. Studies show that the metabolic potential of different tissues of the shrew is very high compared to other small mammals, including rodents [22, 32]. At the same time, the concentration of α-tocopherol of young shrews caught in autumn in the heart, which together with the brain consumes the greatest amount of energy, was significantly lower than in bank-vole underyearlings of different generations. The reasons for the relatively low level of vitamin E in the heart of shrews in the autumn require special research.

Thus, the concentration of vitamins A and E in the tissues of the bank vole and the common shrew depends on a number of factors: species, physiological, seasonal, trophic, etc. In the bank vole, the definitive level of vitamins in organs and tissues is probably formed at an early age and subsequently remains quite stable. More pronounced age-related changes in the level of vitamins in tissues were found in the shrew and are obviously associated with seasonal changes in metabolism and the ecological characteristics of the species. The ecological and physiological traits inherent in different animal species determine the adaptive potential of the species and affect the age-related characteristics of the concentration of vitamins in organs and tissues. The level of vitamins A and E detected in the bank vole and the common shrew at different stages of ontogenesis can be considered a factor of biochemical homeostasis, due to the difference in the level of metabolic processes in different species of small mammals. The high resistance of mammals living in the north to environmental conditions is not limited only to morphological or physiological changes, but is also maintained through biochemical adaptations.

CONCLUSIONS

As a result of the study, the concentration of vitamins A and E in the organs of the bank vole and the common shrew was determined. Despite the fact that the studied species belong to different orders, the distribution of vitamin A in tissues was similar, with the highest retinol concentration observed in the liver and the lowest in the heart. Both species showed age-related differences in retinol levels in the kidneys. Shrews of different ages differed in terms of the vitamin A concentration of their skeletal muscle. Age-related changes in the vitamin E concentration in the tissues of the bank vole and the common shrew had different patterns. In overwintered shrew individuals, a higher tocopherol concentration in tissues was found compared to underyearlings on the eve of wintering, while no age differences were found in bank voles. In general, the conducted comparative study shows a specific profile of vitamins in the organs of the studied species. The identified interspecific differences in the concentration of vitamins A and E in the tissues of the bank vole and the common shrew are probably a reflection of the evolutionary relationships between the organism and the environment, which ensure the most efficient functioning of the metabolic systems of the body in small mammals from different ecological groups at the northern periphery of their range.

FUNDING

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

The work was carried out in accordance with ethical standards approved by the legal acts of the Russian Federation, the principles of the Basel Declaration and the recommendations of the ethical committee of the Institute of Biology of the Karelian Research Center, Russian Academy of Sciences (protocol no. 3 of August 14, 2023).

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

REFERENCES

1. Safronov, V.M., Adaptive features of thermoregulation and maintenance of energy balance in mouse-like rodents, *Vestn. Tomsk. Gos. Univ. Biol.*, 2009, vol. 4, no. 8, pp. 47–61.
2. Schaeffer, P.J., O'Mara, M.T., Breiholz, J., Keicher, L., Lázaro, J., Muturi, M., and Dechmann, D.K.N., Metabolic rate in common shrews is unaffected by temperature, leading to lower energetic costs through seasonal size reduction, *R. Soc. Open Sci.*, 2020, vol. 7, no. 4, p. 191989.
3. Gliwicz, J. and Taylor, J.R.E., Comparing life histories of shrews and rodents, *Acta Theriol.*, 2002, vol. 47, no. 1, pp. 185–208.
4. Rogovin, K.A., Bushuev, A.V., Khruscheva, A.M., and Vasilieva, N.Y., Resting metabolic rate, stress, testosterone, and induced immune response in spring-and fall-born males of Campbell's dwarf hamsters: Maintenance in long-day conditions, *Biol. Bull. Rev.*, 2014, vol. 4, no. 3, pp. 181–191.
5. Bashenina, N.V., *Puti adaptatsii myshevidnykh gryzunov* (Ways of Adaptation of Mouse-Like Rodents), Moscow: Nauka, 1977.
6. Ivanter, E.V., *Ocherki populyatsionnoi ekologii melkikh mlekopitayushchikh na severnoi periferii areala* (Essays on the Population Ecology of Small Mammals on the Northern Periphery of Their Range), Moscow: KMK, 2018.
7. Tarakhtii, E.A. and Davydova, Yu.A., Seasonal variation in hematological indices in bank vole (*Clethrionomys glareolus*) in different reproductive states, *Biol. Bull.*, 2007, vol. 34, no. 1, pp. 9–19.
8. Novikov, E.A., Kondratyuk, E.Yu., and Petrovskii, D.V., Effect of the life history pattern on bioenergetic parameters of northern red-backed voles (*Myodes rutilus* Pall.) in a mountain taiga population from the south of Western Siberia, *Russ. J. Ecol.*, 2015, vol. 46, no. 5, pp. 476–480.
9. Campbell, K.L., Signore, A.V., Harada, M., and Weber, R.E., Molecular and physicochemical characterization of hemoglobin from the high-altitude Taiwanese brown-toothed shrew (*Episoriculus fumidus*), *J. Comp. Physiol.*, 2012, vol. 182, no. 6, pp. 821–829.
10. Ribot, J., Felipe, F., Bonet, M.L., and Palou, A., Changes of adiposity in response to vitamin A status correlate with changes of PPARγ2 expression, *Obes. Res.*, 2001, vol. 9, no. 8, pp. 500–509.
11. Sprenger, R.J., Tanumihardjo, S.A., and Kurtz, C.C., Developing a model of vitamin A deficiency in a hibernating mammal, the 13-lined ground squirrel (*Ictidomys tridecemlineatus*), *Compar. Med.*, 2018, vol. 68, no. 3, pp. 196–203.
12. Kalabukhov, N.I., *Spyachka mlekopitayushchikh* (Mammal Hibernation), Moscow: Nauka; 1985.
13. Karaseva, E.V., Telitsyna, A.Yu., and Zhigal'skii, O.A., *Metody izucheniya gryzunov v polevykh usloviyakh* (Methods for Studying Rodents in the Field), Moscow: LKI, 2008.
14. Tupikova, N.V., Sidorova, G.A., and Konovalova, E.F., *Opredelenie vozrasta lesnykh polevok. Fauna i ekologiya gryzunov* (Determining the Age of Forest Voles. Fauna

and Ecology of Rodents), Moscow: Mosk. Gos. Univ., 1970, pp. 160–167.

15. Ivanter, E.V., *Populyatsionnaya ekologiya melkikh mlekopitayushchikh taezhnogo Severo-Zapada SSSR* (Population Ecology of Small Mammals in the Taiga Northwest of the USSR), Leningrad: Nauka, 1975.
16. Olenev, G.V., Alternative types of ontogeny in cyclomorphic rodents and their role in population dynamics: An ecological analysis, *Russ. J. Ecol.*, 2002, vol. 33, no. 5, pp. 321–330.
17. Olenev, G.V., Determining the age of cyclomorphic rodents: Functional-ontogenetic determination, ecological aspects, *Russ. J. Ecol.*, 2009, vol. 40, no. 2, pp. 93–104.
18. Skurikhin, V.N. and Dvinskaya, L.M., Determination of α-tocopherol and retinol in the blood plasma of farm animals using microcolumn high-performance liquid chromatography, *S.-kh. Biol.*, 1989, vol. 4, pp. 127–129.
19. Il'ina, T.N., Ilyukha, V.A., Baishnikova, I.V., Belkin, V.V., Sergina, S.N., and Antonova, E.P., Antioxidant defense system in the tissues of semi-aquatic mammals, *Zh. Evol. Biokhim. Fiziol.*, 2017, vol. 53, no. 4, pp. 251–256.
20. Ivanter, E.V., Experience in ecological analysis of morphophysiological characteristics of small mammals, *Uch. Zap. Petrozavodsk. Univ.*, 2018, no. 3(172), pp. 7–19.
21. Nieminen, P. and Hyvarinen, H., Seasonality of leptin levels in the BAT of the common shrew (*Sorex araneus*), *Z. Naturforsch C. J. Biosci.*, 2000, vol. 55, nos. 5–6, pp. 455–460.
22. Ivanter, E.V., Ivanter, T.V., and Tumanov, I.L., *Adaptivnye osobennosti melkikh mlekopitayushchikh: Ekologo-morfologicheskie i fiziologicheskie aspekty* (Adaptive Features of Small Mammals: Ecological, Morphological and Physiological Aspects), Leningrad: Nauka, 1985.
23. Kiselev, S.V., Interannual variability in the energy reserves of Laxmann's shrew (*Sorex caecutiens*) on the northern coast of the sea of Okhotsk, *Biol. Bull.*, 2022, vol. 49, no. 2, pp. 107–116.
24. Solomonov, N.G. and Popov, M.V., Ecological, physiological and morphological adaptations of Yakut mammals to winter conditions, in *Adaptatsiya zhivotnykh k zimnim usloviyam* (Adaptation of Animals to Winter Conditions), Sokolov, V.E., Ed., Moscow: Nauka, 1980, pp. 109–116.
25. Mordosov, I.I. and Prokop'ev, N.P., *Populyatsionnaya ekologiya gryzunov Leno-Vilyuiskogo mezhdurech'ya* (Population Ecology of Rodents in the Lena–Vilyui Interfluve), Yakutsk: Sev.-Vost. Fed. Univ., 2021.
26. Mercader, J., Ribot, J., Murano, I., Felipe, F., Cinti, S., Bonet, M.L., and Palou, A., Remodeling of white adipose tissue after retinoic acid administration in mice, *Endocrinology*, 2006, vol. 147, no. 11, pp. 5325–5332.
27. Hyvärinen, H., Brown fat and the wintering of shrews. Advances in the biology of shrews, in *Carnegie Mus. Nat. Hist. Spec.*, Merritt, J.F., Kirkland, G.L., Jr., and Rose, R.K., Eds., Pittsburgh, 1994, vol. 18, pp. 259–266.
28. Keicher, L., O'Mara, M.T., Voigt, C.C., and Dechmann, D.K., Stable carbon isotopes in breath reveal fast metabolic incorporation rates and seasonally variable but rapid fat turnover in the common shrew (*Sorex araneus*), *J. Exp. Biol.*, 2017, vol. 220, no. 15, pp. 2834–2841.
29. Hissa, R. and Tarkkonen, H., Seasonal variations in brown adipose tissue in two species of voles and the common shrew, *Ann. Zool. Fenn.*, 1969, vol. 6, pp. 444–447.
30. Hindle, A.G., Lawler, J.M., Campbell, K.L., and Horning, M., Muscle senescence in short-lived wild mammals, the soricine shrews *Blarina brevicauda* and *Sorex palustris, J. Exp. Zool. A Ecol. Genet. Physiol.*, 2009, vol. 311, no. 5, pp. 358–367.
31. Hollander, D. and Dadufalza, V., Lymphatic and portal absorption of vitamin E in aging rats, *Dig. Dis. Sci.*, 1989, vol. 34, no. 5, pp. 768–772.
32. Stewart, J.M., Woods, A.K., and Blakely, J.A., Maximal enzyme activities, and myoglobin and glutathione concentrations in heart, liver and skeletal muscle of the Northern Short-tailed shrew (*Blarina brevicauda*; Insectivora: Soricidae), *Comp. Biochem. Physiol. B*, 2005, vol. 141, no. 3, pp. 267–273.