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Species composition, abundance and spatial structure of bat community hibernating in Tanechkina and Staroladozhskaya Caves, Leningrad Region, Russia

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ABSTRACT. The paper presents the results of studies of bats hibernating in the Staroladozhskaya and Tanechkina caves in Leningrad Region, Russia. Species composition, abundance, peculiarities of bats' spatial distribution, and microclimatic conditions in the caves were studied in 2003 and 2018–2022. Six species of bats were recorded: *Myotis daubentonii*, *M. dasycneme*, *M. brandtii/mystacinus*, *M. nattereri*, *Plecotus auritus*, and *Eptesicus nilssonii*. The most significant species diversity and abundance of bats were noted in the Tanechkina Cave, which is one of the longest in Leningrad Region. The number of hibernating bats has increased nearly fivefold since 2003, with circa 1900–2500 bats utilizing the cave presently. The composition of species abundance has changed over the years. In 2003, *M. daubentonii* and *M. dasycneme* predominated by number; whereas at the present, *M. dasycneme* comprises more than 70% of the total number of bats. The data on changes in the spatial structure of one of the largest bat communities in Leningrad Region over the period of ten years are presented in our paper for the first time.

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KEY WORDS: Chiroptera, hibernation, spatial structure, *Myotis dasycneme*, *Myotis daubentonii*.

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Видовой состав, численность и пространственная структура сообщества рукокрылых, зимующих в Танечкиной и Староладожской пещерах, Ленинградская область, Россия

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РЕЗЮМЕ. В работе представлены результаты исследований зимовки рукокрылых в Ленинградской области в пещерах Староладожская и Танечкина. Изучение видового состава, численности, особенностей размещения летучих мышей и микроклиматических условий в подземельях было проведено в 2003 и 2018–2022 гг. Зарегистрировано 6 видов рукокрылых: *Myotis daubentonii*, *M. dasycneme*, *M. brandtii/mystacinus*, *M. nattereri*, *Plecotus auritus*, *Eptesicus nilssonii*. Большее видовое разнообразие и большее количество рукокрылых отмечено в Танечкиной пещере, являющейся одной из самых протяженных штолен Ленинградской области. Численность зимующих рукокрылых увеличилась почти в пять раз с 2003 г, на данный момент в пещере насчитывается порядка 1900–2500 летучих мышей. Произошли изменения в численном соотношении разных видов. В 2003 г. по количеству особей лидировали два вида — *M. daubentonii* и *M. dasycneme*, теперь более 70% от общего числа рукокрылых составляет *M. dasycneme*. В статье впервые проанализированы изменения в пространственной структуре одного из самых крупных сообществ рукокрылых Ленинградской области, произошедшие за более чем десятилетний период.

KEY WORDS: Chiroptera, зимовка, пространственная структура, *Myotis dasycneme*, *Myotis daubentonii*.

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Introduction

Bats (Mammalia, Chiroptera) being the second largest order of mammals (IUCN SSC Bat Specialist Group, https://www.iucnbsg.org) have a worldwide distribution and wide ecology range, which leads to facing different threats. In the boreal zone, where seasons vary extremely in their characteristics, bats meet with a spectrum of challenges, e.g. seasonal decrease in availability of food, uncomfortably low temperatures forcing increased energy costs, lack of suitable shelters needed to survive winter, etc. As a consequence, boreal bats utilize two strategies of overcoming these threats — migration and hibernation (Fleming, 2018; Boyles *et al.*, 2019). The latter is a torpor state which is characterized by low body temperature close to the ambient environment and reduced metabolism rates. Hibernation is not a cost-free strategy, because it can lead to an increased probability of predation and freezing (Boyles *et al.*, 2019; Verhees *et al.*, 2022), and suppressed immunity (Whiting-Fawcett *et al.*, 2021). Therefore, bats tend to hibernate in places with reduced exposure to the harsh environment, but with stable microclimate (air temperature a few degrees above zero and high humidity), such as natural and artificial caves, bunkers, fortifications, cellars (Vintulis & Petersons, 2014; Vlaschenko & Naglov, 2018; Verhees *et al.*, 2022).

Monitoring bats at their wintering sites is one of the methods to identify bat population fluctuations (Meyer, 2015; Martinkova *et al.*, 2020; Wegiel *et al.*, 2021). Generally, it is a research in large hibernacula, where hundreds to thousands of animals aggregate, that allows receiving representative data and detecting certain population trends (Lutsar *et al.*, 2000; Smirnov *et al.*, 2007; Piksa & Nowak, 2013; Smirnov *et al.*, 2017; Bernard *et al.*, 2019), though in some cases long-term monitoring in small hibernacula may also reveal strong patterns in population dynamics (Dzieciolowski *et al.*, 2022; Verhees *et al.*, 2022). As a result of such studies, which have begun to be actively conducted in Europe since the 1980s, for some species a positive population dynamics was revealed (Zima *et al.*, 1994; Uhrin *et al.*, 2010; Piksa & Nowak, 2013; Van der Meij *et al.*, 2015; Wegiel *et al.*, 2021), while populations of other species were observed to decrease (Kervyn *et al.*, 2009; Spitzenberger & Engelberger, 2013; Van der Meij *et al.*, 2015). We consider the data on the population dynamics of the large bat community in the northwest of Russia to contribute to the future studies of bat population trends.

There are ten currently confirmed species of bats in the Leningrad Region; three of them are considered as migratory — *Pipistrellus nathusii* (Keyserling et Blasius, 1839), *Nyctalus noctula* (Schreber, 1774) and *Vespertilio murinus* (Linnaeus, 1758). The other seven species are assumed to be sedentary and to hibernate in the region: *Myotis dasycneme* (Boie, 1825), *M. daubentonii* (Kuhl, 1817), *M. nattereri* (Kuhl, 1817), *M. mystacinus* (Kuhl, 1817), *M. brandtii* (Eversmann, 1845), *Plecotus auritus* (Linnaeus, 1758) and *Eptesicus nilssonii* (Keyserling et Blasius, 1839) (Novikov *et al.*, 1970; Strelkov & Buntova, 1982; Bogdarina & Strelkov, 2003). Hibernation period varies in different species, on average, bats begin to appear at hibernation sites from the end of September and can stay there till April; *M. nattereri* are an exception, because they arrive late in January–February, and escape in March (Strelkov, 1971). In 2007–2009, Kovalyov and Popov conducted more detailed research on *M. dasycneme*, which revealed that first individuals appeared in the last decade of September, the significant number of bats was registered starting from the first days of October, the majority of them stayed till the middle of April, and a dozen of individuals were found in the cave till the last decade of May (Kovalyov & Popov, 2011).

The north-west of Russia, in particular Leningrad Region, is poor in natural caves; those which are present have small size and unstable structure, the current length of the biggest natural cave in the Leningrad Region is ca. 130 m (Agapov, 2012). On the other hand, there are more than 50 artificial caves (abandoned mines) in the region, their length varies from several meters to several kilometers (Panteleikov, 2016). According to the previous research, taken all together there were less than 30 undergrounds with suitable characteristics, where hibernating bats were regularly registered (Strelkov, 1958; Chistyakov, 2001; Kovalyov, 2017); for today, at least seven of these hibernacula were ruined.

At present, there are five cave groups (complexes) in the Leningrad Region, each including from two to seven caves that play an important role as bat hibernacula. For bat researchers, two of them, namely caves near Ulyanovka settlement (Sablinskie Caves) and near Staraya Ladoga Village have always been the most interesting because of bat abundance and species composition there. The former were the main overwintering place for *M. nattereri*, the latter were known as the main hibernacula for *M. dasycneme* (Strelkov, 1958; Chistyakov, 2001; Kovalyov, 2017). Nowadays, according to our annual winter bat census in the caves of the Leningrad Region, 99% of *M. nattereri* registered in 2019–2021 still used Sablinskie Caves, and 99% of *M. dasycneme* hibernated in the cave near Staraya Ladoga village (Matlova *et al.*, 2022).

It is noteworthy to mention, that these caves are the only known big undergrounds in Leningrad Region and surrounding Russian territories. In Pskov, Novgorod and Vologda regions, the length of natural cavities does not exceed 20 m, despite the presence of the karst and pseudokarst processes (Agapov *et al.*, 2013), and bat hibernation has not been studied there yet. In Karelia, there were up to 25 bats of 5 species overwintering in the biggest described hibernaculum (Ruskeala) (Belkin *et al.*, 2019). The nearest place where mass bat hibernation was observed is Piusa caves in Estonia, located 300–350 km southwest from the large caves of Leningrad Region. The wintering population there exceeded 3000 bats, with *E. nilssonii* and *M. daubentonii* forming the bulk of the community, and *P. auritus* along with *M. dasycneme* being the second ones in abundance (Lutsar *et al.*, 2000).

In 2003 and 2018–2022, we conducted a series of censuses of bats wintering in the caves near the Staraya Ladoga Village. The main subject of our interest was the Tanechkina Cave, one of the largest caves in the Leningrad Region. We decided to include the Staroladozhskaya Cave into this research as well despite its small size, because it is the nearest bat winter shelter to the Tanechkina Cave and used to be ignored by bat researchers owing to the presence of the big hibernacula nearby.

The first thorough studies of wintering bats in these sites were carried out by Petr Strelkov (1958, 1961, 1965, 1971, 1974). He revealed that up to several hundred of bats of five species wintered annually in these caves, as follows: pond bat (*M. dasycneme*), Daubenton's bat (*Myotis daubentonii*), whiskered bat (*M. mystacinus*), brown long-eared bat (*Plecotus auritus*), and northern bat (*Eptesicus nilssonii*). Later, in the 1970s–1980s, when *M. mystacinus* began to be considered as a complex of species (Strelkov & Buntova, 1982), it became clear that those caves were occupied by Brandt's bat (*M. brandtii*), whereas *M. mystacinus* was proclaimed to be rare in the region (Strelkov & Buntova, 1983).

The current study aims at obtaining up-to-date data on species diversity, abundance, and spatial structure, and revealing changes that occurred in bat community over 15 years. The following tasks were set: to conduct a census of the abundance and species composition of bats; to detect factors affecting spatial distribution of bats within the caves; to compare the results with published data on these hibernacula.

Materials and methods

Study site

Both caves are located 120 km to the east of Saint Petersburg, in Leningrad Region, Russia, near the Staraya Ladoga Village, on the left bank of the Volkhov River. The caves have an artificial nature, they are former glass sand mines with a horizontal structure without vertical passages. The exact time of the end of their exploitation is unknown but the caves are assumed to be abandoned in the middle of the XIX century (Strelkov, 1958; Kovalyov, 2017).

The Tanechkina Cave is located 1.5 km from the Staraya Ladoga Village. According to various estimates, the total length of its passages is about 5500–6500 m (Panteleikov, 2016; Kovalyov, 2017). The height of the cave varies in different parts extremely. The north-western part is very low, from 0.4 to 1 m, and it keeps on decreasing annually due to the ceiling collapse and regular sand deposition by the stream flowing into the cave. The eastern half of the cave has relatively high passages up to 3.3 m. The average height of the cave is 1.6 m. More than 60% of the cave is occupied by underground lakes, whose depth and size varies depending on melt-water and rain. The deepest part of the lake is in the southeastern area of the cave; the depth of the water there was 1.5 m (Kovalyov, 2017). During the spring snow melting, the water level rises.

The Tanechkina Cave has a “difficult to navigate” structure; initially, it seemed to consist of parallel passages, and their arches were supported by numerous columns. However, due to the ceiling and columns collapsing, at the moment the cave has become a complicated labyrinth. In some places, the ceiling fall has formed “islands” in the underground lakes.

The Staroladozhskaya Cave is situated in the village and has a total length of passages of about 400 m, a maximum length from the north to the south is about 50 m, and an average ceiling height of 1.9 ± 0.1 m. An underground lake with a maximum depth of approximately 1 m spreads over almost the entire cave.

Both caves are exposed to hazards of both anthropogenic and natural origins. Despite they are located within the special protected area borders, no practical measures are taken to prevent damage from human activities and degradation with the course of time.

Temperature and humidity

Air temperature was measured in 2018–2022 with an aspiration psychrometer MV-4-M (USSR). Due to the methodological difficulties (the weight of the psychrometer is ca. 1.2 kg, hence it is impossible to put it into any natural crevice in the unstable sandy walls of the cave; it is forbidden to hold the psychrometer in arms during measurements because of the risk of gaining an incorrect data; it is troublesome to use a tripod in order to put the psychrometer on it because of the sticky mud on the floor and flooded parts of the cave) there was only one option to locate the psychrometer at a height of 5–10 cm from the floor. In the flooded parts of the cave, the measurements were carried out 10–20 cm above the water surface. The measurements covering the entire area of the Tanechkina Cave were fulfilled three times: February 2021, December 2021, and February 2022.

The air humidity was calculated based on the psychrometer data using an online calculator on the website https://planetcalc.ru/246/. To compare the results obtained during different survey periods, we made measurements at the same points every time.

Data on weather conditions in the area of the Staraya Ladoga Village (Volkhovsky District of Leningrad Region) were taken from the website https://rp5.ru.

Bat surveys

In 2003, the bat census was carried out at the end of February. In 2018–2022, the surveys were organized twice a year: the first one from the end of November to the early December, the second one from the late January to February throughout.

When determining the species, non-invasive techniques based on external signs and excluding direct contact were used. In 2003, *Myotis brandtii* were examined in more detail to identify the possible presence of *M. mystacinus*. For this purpose, bats were handled and their teeth were examined, thus the size of the cingulum cusp of the upper third premolar was used to distinguish between the species (Strelkov & Buntova, 1982). After the procedure, bats were put back to the same spot they were taken from. In 2018–2022, animals of these species were referred to as the *M. brandtii/mystacinus* group.

In addition to the abundance and species composition, we registered if bats were hibernating singly or in a group, and the number of individuals in each cluster. Hibernation in a cluster was considered to be those cases when animals wintered touching each other. Aside from that, we described if the shelters were used, and measured the distance from the floor to a bat. We mapped all the sites where any bat was detected for further analysis of their spatial distribution. In the Tanechkina Cave, the location of bats was mapped in February 2003 and February 2021.We want to warn the readers that the maps of the Tanechkina Cave used in this paper are only schematic and may not reflect the structure of the cave in full detail.

Statistical analysis

The total number in the abundance analysis covered all alive bats. In order to determine the population dynamics, along with our data we used already published data, namely we took the number of *M. dasycneme*, *M. daubentonii*, *M. brandtii/mystacinus*, *P. auritus* from Strelkov (1958) for 1954–1955, from Chistyakov (2001) for 1997–1998, from Chistyakov & Nikulin (2010) for 1998–1999, 1999–2000 and 2008–2009, and from Kovalyov *et al.* (2014) for 2013–2014.

An assessment of the normality of the data was performed via Shapiro–Wilk test (the size of our samples $n<50$). The significance of differences between samples was evaluated using paired T-test in case of assessment of the abundance of bats at the beginning and end of winter, and comparison between the ratio of bats in flooded and dry parts of the cave.

To classify the preferences of bats hibernating at different heights in 2003 and 2018–2022, a joining cluster analysis (tree clustering) was applied. For each of the given species and each year we calculated the triple of proportions of bats found at the levels (0–1.5m), (1.5–2m) and (>2m) respectively (see Appendix). Then, we applied the Ward's methods to this data with Euclidean distances as distance measure. To make this method clear, let us sketch how Ward's method was implemented. The procedure is recursive. In the beginning we declared that each triple of proportions forms a separate cluster. This followed by a number of steps: on each step we compared all the clusters in the current set of clusters pairwise, found the pair of clusters with the minimal cluster distance between them and merged the clusters in this pair. We stopped when all the data was finally merged into a single cluster.

To reveal any relations between the temperature within the cave and the ambient temperature, a Spearman correlation coefficient was used. The significance level for all cases was stated as $p \leq 0.05$. All calculations were conducted in the Statistica software (version 8.0. for Windows).

Results

Species composition

The bat species composition of two examined neighbouring caves varied insignificantly. During the entire period of our research, four species of bats were recorded in the Staroladozhskaya Cave: *Plecotus auritus*, *Myotis daubentonii*, *M. brandtii/mystacinus* and *Eptesicus nilssonii*. In the Tanechkina Cave, we found six species overall; in addition to four mentioned above, there were *M. dasycneme* and *M. nattereri* as well.

Bat abundance and species proportion

In the Tanechkina Cave, there were 541 individuals in February 2003 (Tab. 1). 16 years later, in December 2018, we recorded a more than threefold increase in the number of bats hibernating there; thus 1733 individuals were found. From 2018, we noted a regular annual increase in the abundance. The number of bats reached its maximum of 2508 specimens in December 2021.

In 2003, *M. dasycneme* and *M. daubentonii* were the most abundant species there, while *M. brandtii* and *E. nilssonii* were rare (Tab. 1). All individuals of *M. brandtii* were examined during this census; *M. mystacinus* was not found among them.

In 2018, *M. dasycneme* formed 85% of the total abundance of bats. The number of this species has increased more than fivefold compared to the results of 2003. From 2019–2020, the number of *M. daubentonii* began to grow, changing the species proportion slightly. Positive population dynamics was revealed in *M. brandtii/mystacinus*; the abundance of hibernating animals of this group increased almost 3 times compared to 2003. The situation was completely different with *P. auritus*. Over the past 15–19 years, its number decreased considerably (from 46 to 9 individuals). *M. nattereri* was found in the Tanechkina Cave occasionally. For the first time, two individuals of these species were found in December 2018. *E. nilssonii* was rarely but regularly registered in the cave.

In the Staroladozhskaya Cave, the maximum number of bats during the period of our observations was 23 individuals, *M. daubentonii* and *P. auritus* were the most common species there (Tab. 2). Their abundance fluctuated from one census to another. In the winter 2021–2022, the long-eared bats almost completely disappeared from this underground.

The number of bats at the beginning and end of winter

The total number of bats in the Tanechkina Cave in 2018–2022 was always higher at the beginning of the winter (in late November–early December). During subsequent February counts we noted a decrease in the number of wintering animals, in 2018–2019 by 352 individuals, in 2020–2021 by 314 individuals, and in 2021–2022 by 115 individuals (Tab. 1).

There were no significant differences in the number of *M. dasycneme* at the beginning and end of winter (T-test, $t = 2.99$, $df = 2$, $p = 0.0959$) though they were quite noticeable. In 2018–2019, the number of pond bats decreased by 24% (351 individuals), in 2020–2021 by 21% (311 individuals); in 2021–2022 the difference comprised only 5% (84 individuals). No such pattern was found for the other species. Changes in the number of *M. daubentonii*, the second most numerous species, were both negative and positive. In 2018–2019, the number of Daubenton's bats increased by 10% (21 individuals), in 2020–2021 it decreased by 4% (13 individuals), in 2021–2022 we recorded a decrease by 6% (32 individuals).

Findings of corpses

Due to the large gap between censuses, we cannot analyse the real mortality rate of bats. In the Tanechkina Cave, dead animals were found during each census in 2018–2022 (Tab. 3). Often, the corpses floating in the water were so abundantly covered in mold that it appeared to be impossible to identify species by visual observations. We did not collect corpses for further identification. The maximum number of corpses found

Table 1. Species composition and number of bats in the Tanechkina Cave (Leningrad Region, Russia) in 2003 and 2018–2022.

Date	*P.aur*	*M.dau*	*M.bran/ M.mys*	*M.das*	*M.nat*	*E.nil*	Not id.	Total
25–26.02.2003	46 (8.5%)	207 (38%)	22 (4.1%)	264 (49%)	0 (0%)	2 (0.4%)	0 (0%)	541 (100%)
07.12.2018	20 (1.2%)	207 (12%)	32 (1.8%)	1.471 (85%)	2 (0.1%)	1 (0.1%)	0 (0%)	1.733 (100%)
01.02.2019	12 (0.9%)	228 (17%)	20 (1.4%)	1.120 (81%)	0 (0%)	1 (0.1%)	0 (0%)	1.381 (100%)
29.11.2019	15 (0.8%)	316 (17%)	47 (2.6%)	1.415 (78%)	1 (0.1%)	3 (0.2%)	8 (0.4%)	1.805 (100%)
11.12.2020	9 (0.5%)	365 (20%)	38 (2%)	1.454 (78%)	0 (0%)	2 (0.1%)	2 (0.1%)	1.870 (100%)
05.02.2021	15 (1%)	352 (23%)	38 (1%)	1.143 (74%)	3 (0.2%)	0 (0%)	5 (0.3%)	1.556 (100%)
10.12.2021	17 (0.7%)	579 (23%)	54 (2.2%)	1.851 (74%)	0 (0%)	2 (0.1%)	5 (0.2%)	2.508 (100%)
18.02.2022	9 (0.4%)	547 (23%)	60 (3%)	1.767 (74%)	0 (0%)	0 (0%)	10 (0.4%)	2.393 (100%)

Notes: P. aur — *Plecotus auritus*, M.dau — *Myotis daubentonii*, M. bran/M. mys — *M. brandtii/ M. mystacinus*, M. das — *M. dasycneme*, M. nat — *M. nattereri*, E. nil — *Eptesicus nilssonii*, Not id. — Not identified.

Table 2. Species composition and number of bats found in the Staroladozhskaya Cave (Leningrad Region, Russia) in 2003 and 2019–2022.

Bat census date	*Plecotus auritus*	*Myotis daubentonii*	*Myotis brandtii/ mystacinus*	*Eptesicus nilssonii*	Total
25–26.02.2003	2 (33%)	4 (67%)	0 (0%)	0 (0%)	6 (100%)
06.12.2019	14 (61%)	9 (39%)	0 (0%)	0 (0%)	23 (100%)
24.01.2020	6 (43%)	8 (57%)	0 (0%)	0 (0%)	14 (100%)
05.12.2020	7 (47%)	5 (33%)	3 (20%)	0 (0%)	15 (100%)
29.01.2021	9 (50%)	8 (44%)	1 (6%)	0 (0%)	18 (100%)
12.12.2021	2 (14%)	8 (57%)	3 (21%)	1 (7%)	14 (100%)
29.01.2022	1 (14%)	6 (86%)	0 (0%)	0 (0%)	7 (100%)

Table 3. Number of bat corpses found in the Tanechkina Cave (Leningrad Region, Russia).

Date	*Myotis dasycneme*	*M. daubentonii*	*M. brandtii/ mystacinus*	Not identified	Total (% of all live animals)
07.12.2018	5	—	—	23	28
01.02.2019	—	—	—	38	38
29.11.2019	—	—	—	8	8
11.12.2020	13	—	1	15	29
05.02.2021	—	2	—	7	9
10.12.2021	18	1	—	10	29
18.02.2022	12	1	—	14	27

at a time was 38 specimens. There were two cases when dead bats were found in the Staroladozhskaya Cave: one corpse of *P. auritus* in December 2021 and one unidentified corpse in January 2022.

Air temperature and humidity within the caves

The following patterns were identified in the Tanechkina Cave. The northern half of the cave was noticeably warmer than the southern one (Fig. 1). The air temperature averaged 7.2 ± 0.1°C (with a minimum of 6.8°C, and a maximum of 8°C at different points). In the central, southern, and southeastern parts of the cave, the air temperature ranged from 6.2 ± 0.1°C to 6.9 ± 0.2°C.

The correlation between the ambient and cave air temperature was determined for the entrance area only (5–7 m from the entrance) (Spearman correlation coefficient, rs = 0.9; r = 0.85; $p \leq 0.05$, $n = 6$). The air temperature was stable in the rest of the cave.

The relative air humidity in the cave was 97–98% on average. The greatest variability of this parameter was observed in the entrance corridors (within 30 m from the entrance), where the humidity ranged from 96% to 100% from one bat census to another.

In the Staroladozhskaya Cave, the data collected in 2019–2022 showed that while the distance from the entrance was increasing, the air temperature increased as well and reached its maximum (5.4–7.7°C) in the most remote part of the underground (Fig. 2). The coldest conditions were close to the entrance, where the temperature ranged from 2.0°C to 2.8°C.

The cave microclimate depended on external ambient temperature strongly, thus the average air temperature in the cave correlated positively with the average monthly temperature of the surrounding area (Spearman correlation coefficient, rs = 0.87; r = 0.85; $p \leq 0.05$, $n = 6$) (Fig. 3).

The air temperature in the cave changed dynamically. In December 2021, the temperature in the entrance area dropped from 4.4°C to 3.4°C within a week. Throughout this week, severe frosts from minus 9°C to minus 22°C continued.

The relative air humidity in the Staroladozhskaya Cave was high between 71% and 100% in different parts of the cave. The average humidity in the cave varied from 95% to 98% from one census to another. In January 2022, relative air humidity was only 89% on average.

Spatial structure of bat community in the Tanechkina Cave

During the course of research, some certain patterns and changes in spatial distribution of bat assemblage in

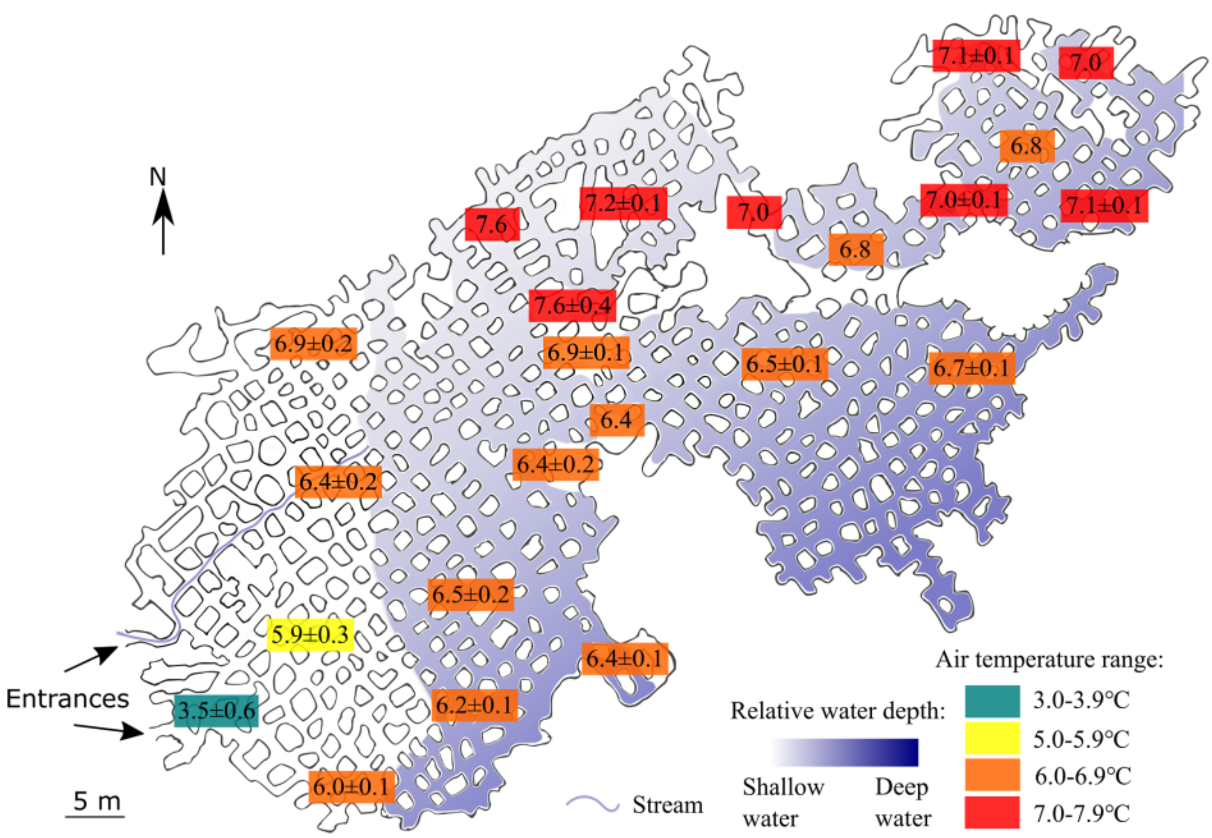

Fig. 1. Plan of the Tanechkina Cave (Leningrad Region, Russia) with the relative depth of the underground lake and the average air temperature (the data collected from 2021 to 2022; $n = 3$ for each measurement point).

the Tanechkina Cave were found. In 2003, more than 80% of the registered *M. dasycneme* hibernated in a relatively small area in the southwestern part of the cave (Fig. 4). Pond bats were often observed in clusters of up to 10–20 animals there. In the other parts of the cave, *M. dasycneme* were less numerous hibernating mostly singly. In the north-eastern and north-western parts of the underground, this species was not detected at all.

In 2021 *M. dasycneme* still concentrated in the southwestern area (Fig. 4). Large aggregations of pond bats occurred in the central part of the cave, mainly above the "islands" — dry areas elevated above the water. In the southeastern part, pond bats began to hibernate in clusters of 3–23 individuals. Single individuals occurred in the northeastern part; several animals were regularly found near the entrance of the cave.

Although the air temperature was measured near the floor, and we cannot observe the entire impact of the microclimate on bats' distribution, there are general tendencies that can be noticed. The bulk of the pond bats' population was located in the area with the average temperature 6.5°C, some individuals were regularly found in the relatively cold entrance area (mean 3.5°C), and several bats hibernated in warmer parts in the north-east with average temperature 7.0–7.6°C (Figs 1, 4).

Despite concentrating in the flooded part of the cave, significantly more *M. dasycneme* were registered above the dry land (T-test, $t = -7.84$, $df = 3$, $p = 0.004$), with 5–23% of bats hibernating above the water.

In 2003, *M. daubentonii* were found mainly in three areas (Fig. 5). Most of the individuals were located in the southeastern part of the mine. The second area, where Daubenton's bats were noted, was in the southwestern part. The animals hibernated no closer than 30 m from the entrance of the cave. The most remote area where this species hibernated was located in the northeastern part. Some individuals were found in the north of the underground.

In 2021, the total number of *M. daubentonii* increased and the space occupied by this species expanded respectively (Fig. 5). The bats began to hibernate at the entrance area of the cave, including in the immediate vicinity of the entrance, displaying the tolerance to rather low temperature (mean 3.5°C). A remarkable number of Daubenton's bats occurred in the central and southwestern parts of the underground with the moderate temperature (6.0–6.9°C). The abundance of *M. daubentonii* also increased in the north. The bats were noticed in the warmer northern and northeastern area as well (7.0–7.6°C). Throughout the entire area of the cave, Daubenton's bats also began to occupy the space along the contour cave walls contrary to 2003. The proportion of bats locating over dry land or water was almost equal.

In 2003, the number of *M. brandtii/mystacinus* wintering in the Tanechkina Cave was small, so it was impossible to draw out the preferences in spatial distribution of this species. This species utilized the southwestern and central areas, avoiding the north of the underground (Fig. 6).

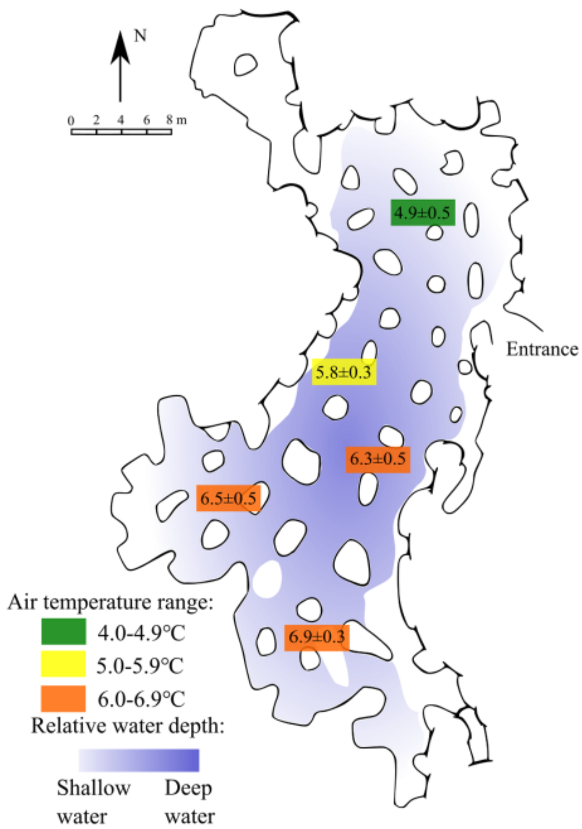

Fig. 2. Plan of the Staroladozhskaya Cave (Leningrad Region, Russia) with the relative depth of the underground lake and the average air temperature ± SE (the data collected from 2019 to 2022; $n = 6$ for every measurement point).

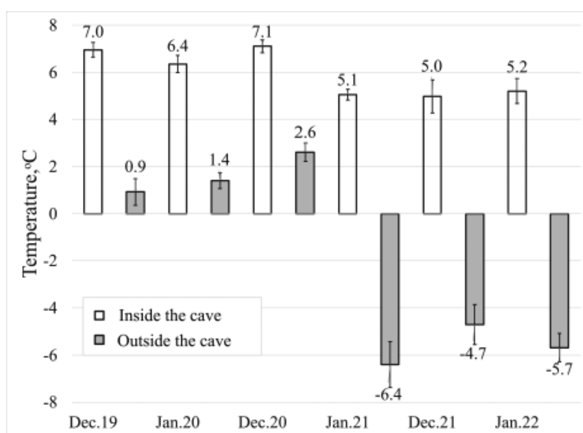

Fig. 3. The average air temperature ± SE in the Staroladozhskaya Cave and near the Staraya Ladoga Village, Leningrad Region, Russia (cave values measured on the day of a census; for the ambient temperature, average values are given for the period of 30 days prior to the day of the census).

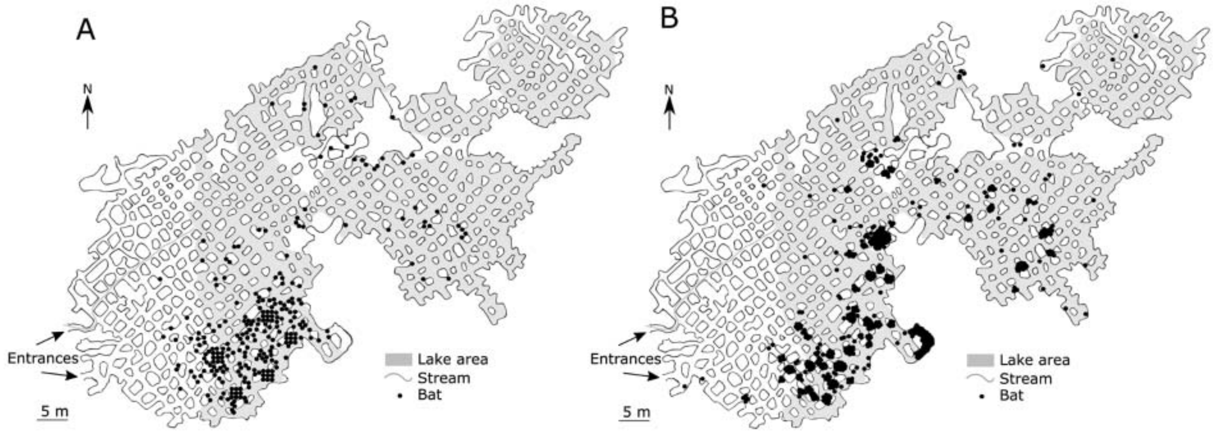

Fig. 4. Distribution of *Myotis dasycneme* in the Tanechkina Cave (Leningrad Region, Russia) in February 2003 (A) and February 2021 (B).

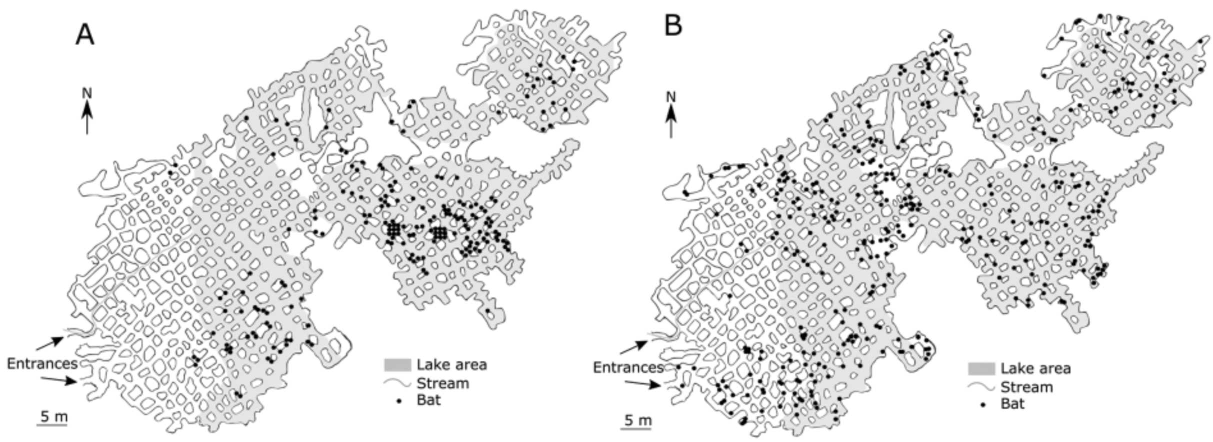

Fig. 5. Distribution of *Myotis daubentonii* in the Tanechkina Cave (Leningrad Region, Russia) in February 2003 (A) and February 2021 (B).

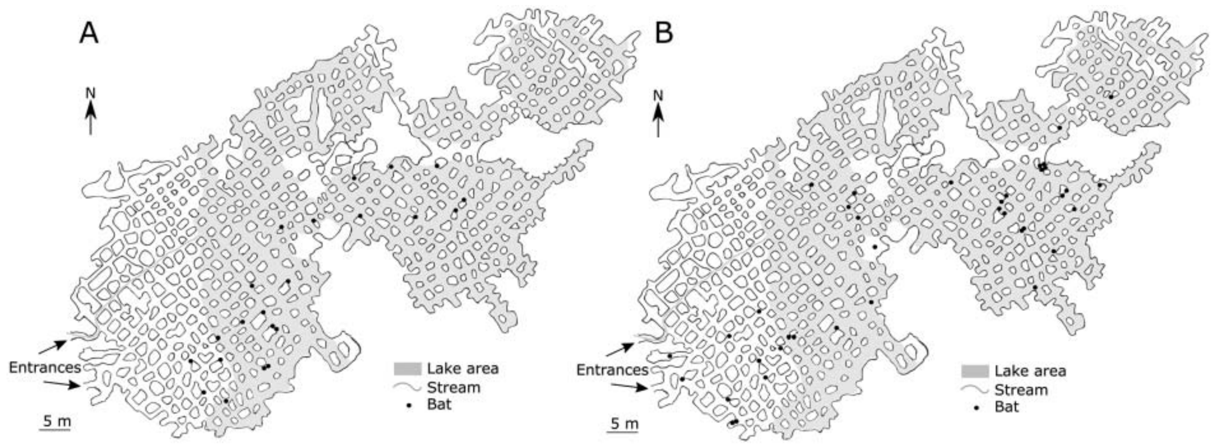

Fig. 6. Distribution of *Myotis brandtii/mystacinus* in the Tanechkina Cave (Leningrad Region, Russia) in February 2003 (A) and February 2021 (B).

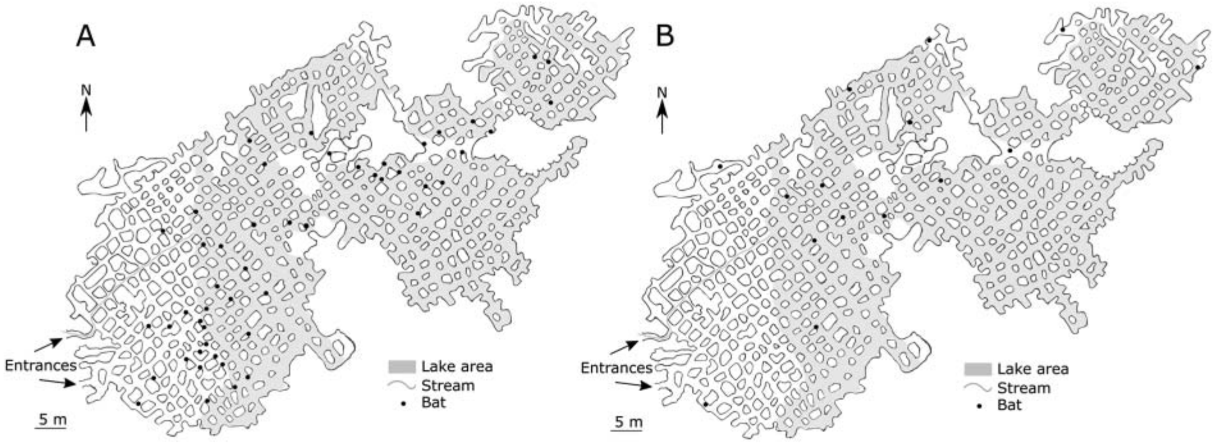

Fig. 7. Distribution of *Plecotus auritus* in the Tanechkina Cave (Leningrad Region, Russia) in February 2003 (A) and February 2021 (B).

18 years later, in 2021, the distribution of *M. brandtii/mystacinus* hardly changed. Most of the individuals were found in the southwestern and southeastern parts with the mean temperature of 6.5°C. Two Brandt's bats were in the warm north-eastern area (mean 7.0°C). There was one individual always registered within 15 m from the entrance (mean 3.5°C). 58% of Brandt's bats located over water.

In 2003, *P. auritus* was found in almost all areas of the Tanechkina Cave except for the southeastern part with high ceilings and the greatest depth of the lake (Fig. 7). Many individuals hibernated in the western half of the cave, where they occupied even low passages.

In 2021, the number of *P. auritus* decreased significantly, thus, no trends in their spatial distribution were observed. Nevertheless, we noted that *P. auritus* almost all disappeared from the southwestern part of the cave (Fig. 7). Registered animals hibernated in the centre with the temperature around 6.5°C and the warmer north of the underground. The majority of bats located over the dry land.

E. nilssonii were always rare (from one to three individuals) in the Tanechkina Cave. In 2003, there were two northern bats in the southwestern area, 10–20 m from the entrance. In February 2021, we did not find this species in the cave. During other censuses in 2018–2022, *E. nilssonii* hibernated in the western half of the mine, at the distance of 15–50 m from the entrance, sometimes on the wall across from it.

Allocation in height

To define if there were any patterns in choice of the distance from the ground to the spot where bats hibernated, we performed a cluster analysis based on the following data (Appendix). In Fig. 8 one can see how the clusters were being merged and in which order, as well as the cluster distance between them.

The two clusters formed on the second to last step and having the biggest difference in the distance between them are of the greatest interest. After looking back into the data (Appendix) we can see that the upper cluster was formed by cases when bats hibernated lower than 1.5 m, while the lower one consisted of cases when bats hibernated higher than 1.5 m.

From 56.3% (in 2003) to 91.7% (in 2019) of *P. auritus* hibernated lower than 1.5 m. Some animals were found at a height of 44 cm, 50 cm, and 60 cm which we assess to be potentially risky in a view of predators. At the same time, no more than 21% of long-eared bats were situated higher than 2 m above the ground. In 2019–2022, *M. daubentonii* and *M. brandtii/ mystacinus* were more often registered lower than 1.5 m compared to 2003 (from 60.8% to 73. 6% for the former; from 40% to 63.2% for the latter).

E. nilssonii were noted at different heights in both caves. In 2003, animals were located between 1.5 and 2 m height; in 2019 a single individual hibernated 1.5 m above the ground; in later years, we did not find this species during February censuses. In November 2019, two individuals were at a height of 1.8 m, one individual — 2.5 m above the ground.

Use of micro-shelters

As micro-shelters, bats used vertical crevices in the walls and arches, domelike niches, horizontal shelves and small cylindrical burrows. The proportion of bats hibernating either openly or using crevices varied over the years.

The majority of *P. auritus*, *M. daubentonii* and *M. brandtii/mystacinus* hibernated openly on the walls. The frequency of use of crevices by *P. auritus* varied from 41.7% to 11.1% in different censuses (Fig. 9). The proportion of *M. daubentonii* and *M. brandtii/mystacinus* hibernating in micro-shelters decreased: from 31.8% in 2003 to 6.6% in 2021–2022 for the former, and from 23.1% to 6.7% for the latter. *M. dasycneme*

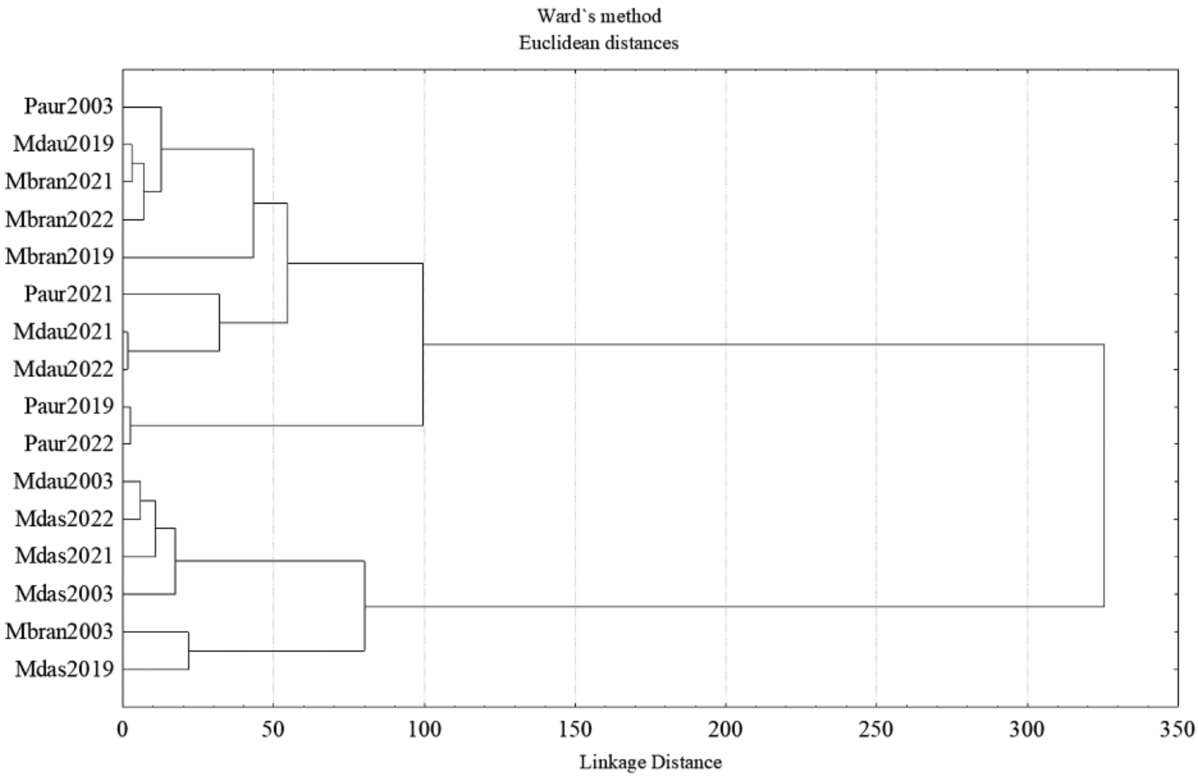

Fig. 8. Cluster analysis (Ward's method) of bats proportion within different height ranges (0–1.5 m; 1.5–2 m; > 2 m) based on February censuses (2003, 2019, 2021, 2022). Mdau — *Myotis daubentonii*, Mdas — *M. dasycneme*, Mbran — *M. brandtii/ mystacinus*, Paur — *Plecotus auritus*.

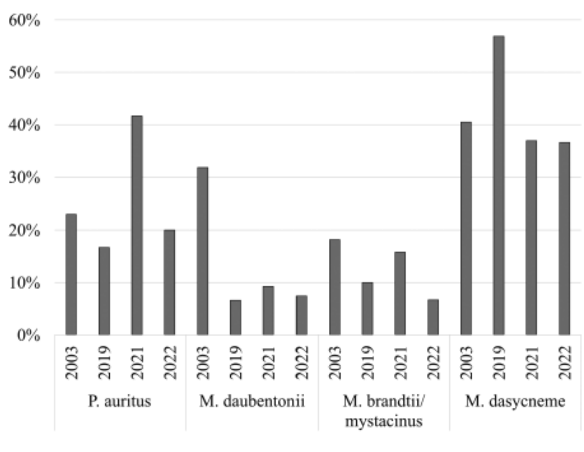

Fig. 9. The frequency of occurrence of bats in micro-shelters in caves near Staraya Ladoga Village, Leningrad Region, Russia (February data).

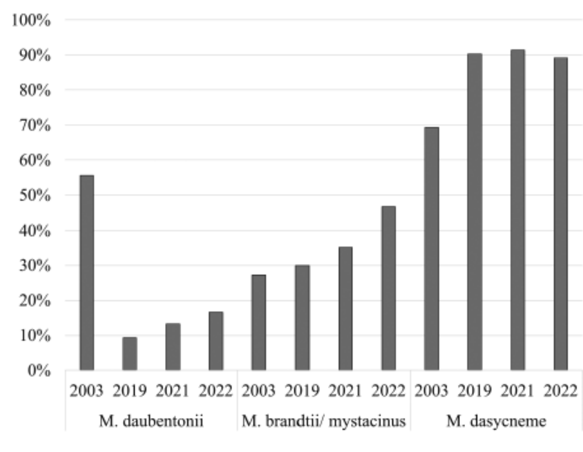

Fig. 10. The frequency of forming clusters by different species in caves near Staraya Ladoga Village, Leningrad Region, Russia (February data).

used crevices and burrows more often than other species. In 2018 and 2019, more than 50% of pond bats were found in shelters. Only one out of three registered *E. nilssonii* hibernated in the crevice (in 2003). Three out of four registered *M. nattereri* were situated in micro-shelters.

Hibernation in clusters

Considering the frequency of aggregation of different species of bats (Fig. 10), the greatest tendency towards hibernation in groups was observed in *M. dasycneme*. The clusters of pond bats were quite numerous. The largest ones included 52 (2019) and 82 (2022) individuals. The groups of 20–30 animals were most common.

In other species, the vast majority of hibernating bats did not form aggregations. In *M. brandtii/ mystacinus*, the occurrence of animals in groups ranged from 27.3% to 46.7% in different years. The number of *M. daubentonii* hibernating in clusters decreased considerably from 55.5% in 2003 to 14.7% in 2022. Both Brandt's bats and Daubenton's bats most commonly assembled in single pieces clusters of 2 individuals, with clusters up to 3–4 animals as a rare case. *P. auritus* and *E. nilssonii* usually did not form single species clusters. We registered a pair of long-eared bats wintering together only once.

Interspecific clusters consisted of *M. dasycneme* and *M. daubentonii* (41.7% cases) mostly. They were less common in *M. dasycneme* and *M. brandtii/ mystacinus* (36.1% cases); in *M. brandtii/ mystacinus* and *M. daubentonii*, they were quite rare (19.4% cases). There was a single case when *P. auritus* hibernated with *M. daubentonii*. Once *M. brandtii/ mystacinus* wintered together with two individuals of *M. nattereri*, and once *E. nilssonii* hibernated together with *M. brandtii*.

Discussion

The Tanechkina Cave has been playing an important role as a hibernaculum in north-western Russia for many decades due to its size and abundance of bats (Strelkov, 1958; Chistyakov, 2001; Belkin *et al.*, 2015; Kovalyov, 2017). Over the past 65–70 years since the first full-done study of the cave, noticeable changes in the bat abundance appeared there. A clear upward long-term trend in *M. dasycneme* and *M. daubentonii* was observed (Fig. 11). The population dynamics of the former is of a particular interest because the current state of *M. dasycneme* in Europe was assessed as Near Threatened due to the low abundance (Hutson *et al.*, 2007). Their population trend at hibernation sites in the number of European countries was defined as stable after a period of the decline (Van der Meij *et al.*, 2015), and in some countries it remains negative (Nistreanu *et al.*, 2022).

In the Tanechkina Cave, nowadays we notice a population development of *M. dasycneme*, the most dramatic increase in the number of pond bats began to be observed within the first decade of the 2000s. Before that, for nearly a 40-year period their abundance

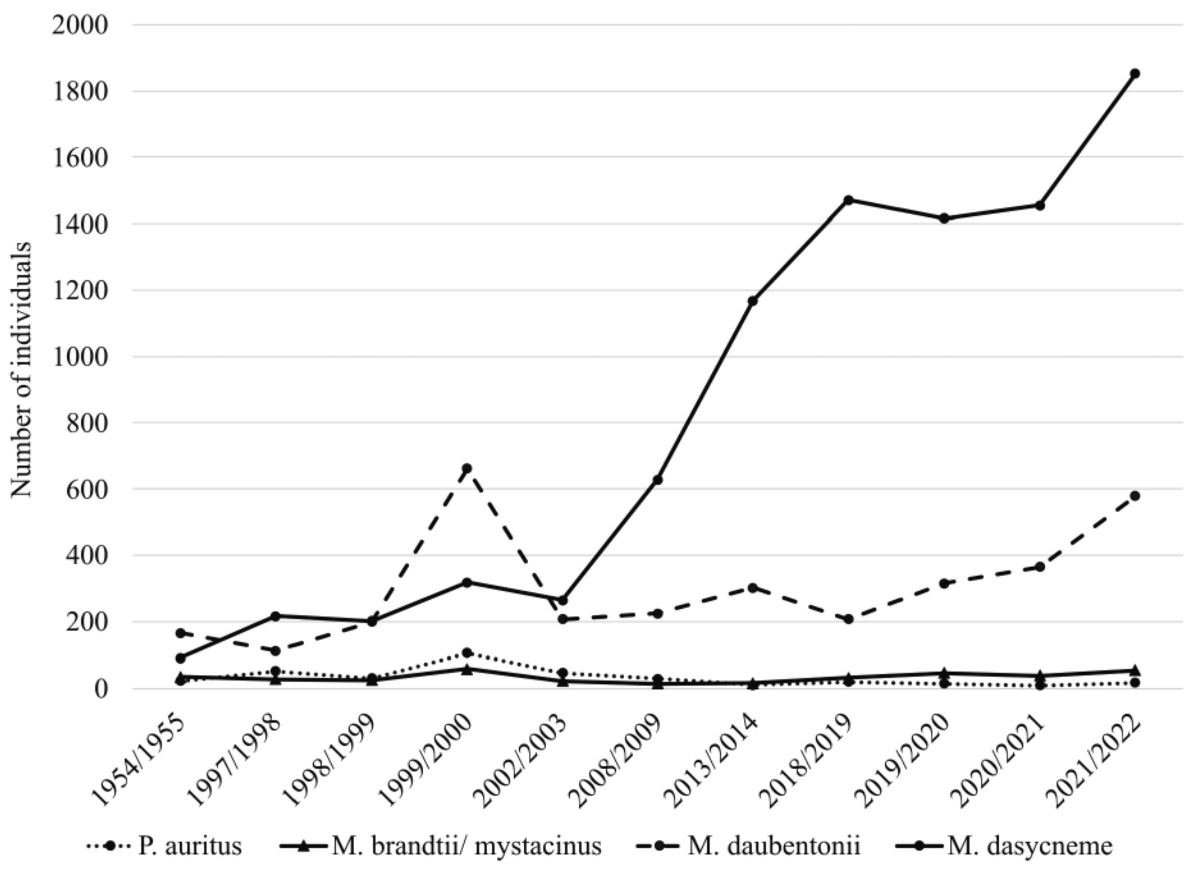

Fig. 11. The dynamics in the abundance of *Myotis dasycneme*, *M. daubentonii*, *M. brandtii/mystacinus* and *Plecotus auritus* in the Tanechkina Cave (Leningrad Region, Russia) from 1954 to 2022. Data from Strelkov (1958) for 1954–1955, from Chistyakov (2001) for 1997–1998, from Chistyakov & Nikulin (2010) for 1998–1999, 1999–2000 and 2008–2009, and from Kovalyov *et al.* (2014) for 2013–2014.

was unknown and, starting from 1997, was slightly increasing (Fig. 11). Regarding the current number of *M. dasycneme*, the Tanechkina Cave today is a unique place with the largest hibernating colony of pond bats in the East of the Baltic region (Lutsar *et al.*, 2000; Baranauskas, 2006a, b; Siivonen & Wermundsen, 2008; Masing *et al.*, 2009; Wermundsen & Siivonen, 2010b; Belkin *et al.*, 2013; Tidenberg *et al.*, 2019). The other known large hibernacula of *M. dasycneme* were reported from the Smolinskaya Cave in the Ural Region with ca. 1730 individuals there in 1998 (Bol'shakov *et al.*, 2005); from two limestone mines Daugbjerg and Mønsted in Denmark with 3400 and 4600 individuals there respectively in 2009 (Baagøe & Degn, 2009); and from the artificial caves of Samarskaya Luka with more than 4000 individuals there in 2016 (Smirnov & Vekhnik, 2011; Smirnov *et al.*, 2017).

The decrease in the abundance of *M. dasycneme* in the second half of winter deserves special attention. A similar pattern was revealed at hibernating sites in Poland. Thus, there were significantly more animals in hibernacula in November–December than in January–February (Ciechanowski *et al.*, 2007). The same phenomenon was noticed in Smolninskaya and Arakaevskaya caves of the Ural Region (Orlov, 2000). In both cases, authors assumed that this casus might be explained by the escape of bats into inaccessible for the researchers parts of the underground or by the movement of bats into the deep crevices.

However, in our studies, almost the entire area of the cave was accessible enough to be inspected. In 2015, the cave was fully re-examined by local speleologists who supplied us with the new plan of the cave, thus the possibility of the presence of the undiscovered part where ca.300 pond bats vanish annually seems unlikely. We cannot deny that there are many crevices in the cave, and some of them are located too high to be well examined, hence, we assume that 1) during each census some part of bats is always overlooked; 2) the observed decrease may be partly explained by bats' escape in these shelters.

Another explanation of the difference in the abundance of pond bats at the beginning and end of winter that should be considered is the possible shift of bats into the alternative hibernacula within the winter months. We assume that the probability of such behaviour is very low due to the following. *M. dasycneme* seems to be a thermophilic cave-dwelling hibernator searching for a proper microclimate (Wermundsen & Siivonen, 2010a; Smirnov *et al.*, 2012); moreover, pond bats usually either avoid using anthropogenic structures for overwintering or hibernate in small numbers in such roosts (Lesinski *et al.*, 2004). In the studied case, the nearest available hibernacula was the Staroladozhskaya Cave situated 1.5 km aside from the Tanechkina Cave. Indeed, in the 1950s, *M. dasycneme* were observed to hibernate in the Staroladozhskaya Cave (Strelkov, 1974). However, after 1956, when all the bats in the cave were intentionally killed by local people, the abundance of bats decreased significantly, and since that Daubenton's bats and brown long-eared bats were the only species to keep on hibernating in this underground (Strelkov, 1974). During our research, pond bats were never registered in this cave (Tab. 2).

It is noteworthy to mention, that the Staroladozhskaya Cave due to the small size and the extremely dynamic response of its microclimate to the changes of the ambient environment (the temperature primarily), has very unstable conditions (Figs 2, 3). Also, there is a high level of the anthropogenic pressure, which disturbs bats during hibernation; it can lead to the changes in species composition within the hibernacula, and in some cases bats escape from their roost for years after strong disturbance (Luo *et al.*, 2013; Doty *et al.*, 2018; Bernard *et al.*, 2019; Bachorec *et al.*, 2021). Hence, this hibernaculum is supposed to be inconvenient for *M. dasycneme* who tends to spend winter in stable environment (Grzywinski *et al.*, 2012).

It appeared that this decrease cannot be associated with the bats' flow into the other caves in Leningrad Region. To begin with, previous research showed that the vast majority of *M. dasycneme* in the region have been hibernating in the Tanechkina Cave (Strelkov, 1958; Chistyakov, 2001; Kovalyov, 2017; Matlova *et al.*, 2022). Furthermore, we carried out censuses of hibernating bats in all the undergrounds of the region known as bat winter shelters simultaneously, and no significant increase in the number of *M. dasycneme* in February was observed there; though the abundance of other species increased in the second half of winter (unpublished data). Aside from hibernacula in the Leningrad Region, the caves in Estonia or hibernation sites in Latvia may be potential places where pond bats might move to. However, after a 50-year period of bat banding in Estonia, when 1309 pond bats were marked, there was no evidence of the presence of Estonian bats at hibernation sites in the Leningrad Region (Masing *et al.*, 1999). In Latvia, there were 436 individuals of *M. dasycneme* banded in 2005–2007 (Vintulis & Šuba, 2010), but there were no recaptures of these individuals in the Tanechkina Cave as well yet.

Among other issues, a high mortality rate may explain the observed decrease. Although there were a relatively small number of corpses found during our censuses (Tab. 3), it is impossible to assess the real mortality rate without special research. We assume that some part of the bats becomes prey for the dogs, cats, ermines and rats, since their tracks were found in the cave. These predators may liquidate the corpses as well as alive bats, changing the observed number of registered bodies. Moreover, considering that the mortality rate in flooded undergrounds was proved to be significantly higher than in "dry" ones (Fritze & Puechmaille, 2018), it can be expected that a significant proportion of bats die during hibernation in the Tanechkina Cave every year.

Anyway, the decrease in the abundance of *M. dasycneme* in the second half of winter has been observed for at least three years straight, and there is a gap in our knowledge of the reasons for this phenomenon. Nevertheless, the observed pattern imposes certain methodological recommendations for winter censuses of pond bats in the region. It seems to be more relevant to carry out the quantification of *M. dasycneme* in the first half of winter. The same suggestion has already been put forward in Ciechanowski *et al.* (2007).

M. dasycneme showed a high level of site fidelity. The majority of individuals concentrated in a small southwestern part of the cave in 2003 as well as in 2021 (Fig. 4). Several reasons may explain such conservatism: the tendency to use particular micro-shelters; the preferences on the microclimate in this part of the underground; and the requirement on clustering. To determine the key factors influencing this conservatism, more research is needed with bat banding and detailed studies of the cave environment. In the artificial caves of Samarskaya Luka, pond bats demonstrated a similar behaviour. Their distribution there was considerably irregular; the species had a high degree of aggregation as well as a tendency to hibernate in ceiling crevices (Smirnov *et al.*, 2012). In 2021–2022, the proportion of pond bats hibernating openly on the wall decreased in comparison with previous years. This may be due to the significant increase in bat abundance along with a limited number of suitable shelters. The temperature fluctuations, the drafts and disturbance can also change the rate of use of micro-shelters by bats (Strelkov, 1958; Bondarenko, 2005).

The most remarkable changes in the spatial structure were noted in *M. daubentonii*. Over the past 18 years since the first detailed mapping, Daubenton's bats dispersed across the cave (Fig. 5). The increased total number of species together with its plasticity in choosing conditions for hibernation — ability to hibernate in a wide range of temperatures in different types of shelters; a slight tendency to form clusters and to use crevices; tolerance to other species presence (Masing & Lutsar, 2007; Siivonen & Wermundsen, 2008; Chistyakov, 2009; Smirnov *et al.*, 2012; Matlova *et al.*, 2020), may be causative for their expansion.

In 2018–2022 compared to 2003, more individuals were registered at a low height. Those changes may be explained by the assumption bats started using low passages along with areas with high ceilings as well as a gradual decrease in the total height of the cave. Additionally, bats may change their preferences in hibernation height range due to the microclimatic fluctuations. We measured the temperature close to the floor, and it was stable almost in the entire cave, with the correlation between the ambient and cave air temperature being determined for the entrance area only (5–7 m from the entrance) (Spearman correlation coefficient, rs = 0.9, r = 0.85, $p \leq 0.05$, $n = 6$). Despite that, it is a vertical gradient of the microclimate and its fluctuations that may influence bat preferences in hibernation height.

It is to be noted that *P. auritus* despite low abundance was observed in all parts of the cave, and it was even registered in the areas with air temperature of +7°C. In Europe, this species shows a tendency to hibernate in relatively small artificial hibernacula, e.g. cellars, wells, attics (Lesinski *et al.*, 2004; Vintulis & Petersons, 2014) along with the ability to survive at quite low temperatures (Masing & Lutsar, 2007; Chistyakov, 2009; Chistyakov & Bogdarina, 2010). Based on the above, it was suggested that *P. auritus* prefers to overwinter in the roosts with relatively low temperatures. However, according to our observations, as well as research conducted in the caves of Samarskaya Luka (Smirnov *et al.*, 2012) and Karelia (Belkin *et al.*, 2021), this species is tolerant to wintering conditions and can hibernate at a wide range of microclimatic conditions.

In 2018, *M. nattereri* was found in the Tanechkina Cave for the first time ever (Strelkov, 1958, 1971, 1974; Chistyakov, 1999, 2001; Chistyakov & Nikulin, 2010; Kovalyov *et al.*, 2014; Kovalyov, 2017). Within Leningrad Region, this species has never been noted in any known hibernacula to the east of 31°E. Most of Natterer's bat population hibernates in the caves near the Sablino Village (Kovalyov, 2017; Matlova *et al.*, 2022), ca. 90 km southwest from the Tanechkina Cave. The presence of occasional individuals of *M. nattereri* may be explained by a general increase in the number of this species in Leningrad Region (Agafonova *et al.*, 2022). Therefore, animals could either search for the new hibernaculum or use it during a nomadic migration. This assumption concurs with the peculiarities of the biology of this species. Thus, in locations with mild temperate winters, in England for instance, *M. nattereri* were observed to hunt throughout the winter during the arousal bouts, with non-volant prey comprising more than 60% of their diet (Hope *et al.*, 2014). Furthermore, this species arrives at hibernation sites later and departs earlier compared to other *Myotis* species at the same range (Reusch *et al.*, 2023), hence proving the ability of Natterer's bats to move between the roosts during the mild winter. Interestingly, a single observation of *M. nattereri* was registered in the Piusa caves in Estonia for over 50-years of observations (Lutsar *et al.*, 2000).

Conclusion

According to the results of our research, the Tanechkina Cave is of the most importance serving as one of the largest known hibernacula of *M. dasycneme* with ca. 1500–1800 individuals currently utilizing it. Regarding the abundance of *M. daubentonii*, *M. brandtii/mystacinus* and *P. auritus* hibernating there, this cave is a significant overwintering roost for bats in the northwest of Russia. At the moment, ca. 1900–2500 bats hibernate there annually.

M. dasycneme showed a high level of conservatism in spatial distribution and, despite the increased number during the last 18 years, the most part of the population still concentrated at a particular area of the cave, occupying the micro-shelters there and forming clusters of different sizes. In contrast to this species, *M. daubentonii*, with great ecological plasticity, began to utilize the entire area of the cave along with the increase in abundance.

Regarding the changes in the number of pond bats during the winter, censuses of *M. dasycneme* should be carried out in November–December, since the number of this species is noticeably decreasing by February. Whereas there were no suitable hibernacula in the close vicinity found as well as unknown parts of the cave where bats could escape in the second half of winter, a high mortality rate might be an explanation for the observed pattern. Nevertheless, this phenomenon still needs to be well studied.

There was no satisfying relation established between mean temperature and bats' locations. The majority of individuals of all species tend to stay within the area with mean temperature around 6.5°C. This area is almost completely flooded except for several halls and patches of dry land. This pattern of bats' distribution might be explained by different reasons, e.g. the safety of the area with impossibility for predators and humans to reach or species-specific tradition. The microclimatic influence is the subject for future research.

Unfortunately, despite being located within the special protected area borders, no practical measures are taken to prevent damage from human activities and degradation with the course of time. In view of the lack of accurate mapping and walls, arcs and ceilings inspection for the traces of devastation and falling, the systematic monitoring of both geological and geotechnical is needed. We discovered the following ecological and geological hazards to be prevented: the sand collapsing which lifts the floor and limits the space for bats; soil erosion along the banks of the Volkhov River that can change the profile of the cave's entrance; the contamination of unspecified nature with the stream flowing into the cave; heavy anthropogenic pressure by visitors with open fire, noise and litter. The reasonable solution might be locking the cave entrance for the hibernation period, keeping it open for the public in summer. Otherwise, the lack of cave conservation management causes a serious concern for the future of these hibernacula and the hibernating colony of bats.

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Appendix. The proportion of bats registered at different height ranges (0–1.5m; 1.5–2m; > 2m) in 2003 and 2019–2022. The order of variables in the two left columns corresponds to the cluster tree (Fig. 8).

Year	Species	0–1.5m	1.5–2m	>2m
2003	*Myotis brandtii*	0%	90.9%	9.1%
2019	*M. dasycneme*	17.6%	80.4%	1.9%
2003	*M. dasycneme*	10.6%	56.1%	33.3%
2021	*M. dasycneme*	22%	58.9%	19.1%
2003	*M. daubentonii*	19.9%	55.5%	24.6%
2022	*M. dasycneme*	20.4%	51.2%	28.4%
2021	*M. daubentonii*	72.9%	24.6%	2.5%
2022	*M. daubentonii*	73.6%	25.1%	1.3%
2021	*Plecotus auritus*	58.3%	20.8%	20.8%
2021	*M. brandtii*	63.2%	36.8%	0%
2022	*M. brandtii*	58.3%	41.7%	0%
2019	*M. daubentonii*	60.8%	37.8%	1.4%
2019	*P. auritus*	91.7%	8.3%	0%
2022	*P. auritus*	90%	10%	0%
2019	*M. brandtii*	40%	60%	0%
2003	*P. auritus*	56.3%	35.4%	8.3%