

Hibernacula of *Myotis* bats in artificial caves in the Leningrad Region

Dmitry N. Kovalyov

ABSTRACT. *Myotis* bats were investigated from all known artificial caves of Leningrad Region. The bat's wintering places (hibernacula) studied during eight seasons from 2007 to 2015 within a long-term bat monitoring effort. The following mouse-eared bat species were found: *Myotis dasycneme* (Boie, 1825) — pond myotis, *M. daubentonii* (Kuhl, 1817) — Daubenton's myotis, *M. nattereri* (Kuhl, 1817) — Natterer's myotis, and species complex *Myotis brandtii/mystacinus* — Brandt's/whiskered myotis. Massive hibernacula of the Natterer's myotis, Brandt's/whiskered myotis, and pond myotis was found within group of Staroladozhskije Caves; namely, Tanechkina Cave at present is a biggest known simultaneously wintering of *Myotis* bats. Hibernacula and their vicinity microclimatic conditions were described with using instrumental measurements of the temperature and humidity. The specific preferences of the studied species were identified that connected with position of hibernating groups relative cave entrances and underground water capacity, specific micro-conditions of temperature and humidity ranging. As result, we have a preliminary assessment of the relationship between the size of the hibernacula and the well-being of the mouse-eared bat populations from territory of Leningrad Region. In addition, we attempted to assessment of a vulnerability of the some hibernating colonies, and, in general, populations of the several studied species.

How to cite this article: Kovalyov D.N. 2017. Hibernacula of *Myotis* bats in artificial caves in the Leningrad Region // Russian J. Theriol. Vol.16. No.1. P.94–109. doi: 10.15298/rusjtheriol.16.1.09

KEY WORDS: *Myotis*, wintering, artificial cave, temperature, humidity, Russia.

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Зимовки ночниц в пещерах-штольнях Ленинградской области

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РЕЗЮМЕ. Исследованы ночницы *Myotis* из всех известных искусственных пещер Ленинградской области. Зимовки летучих мышей (hibernacula) изучались в течение 8 сезонов с 2007 по 2015 г. в рамках долгосрочного мониторинга летучих мышей. Были обнаружены следующие виды ночниц: *Myotis dasycneme* (Boie, 1825) — прудовая ночница, *M. daubentonii* (Kuhl, 1817) — водяная ночница, *M. nattereri* (Kuhl, 1817) — ночница Наттерера, и видовой комплекс *Myotis brandtii/mystacinus* — ночница Брандта/усатая ночница. Внутри группы Староладожских пещер обнаружена массовая зимующая колония ночницы Наттерера, прудовой ночницы и видов комплекса Брандта/усатая; а точнее Танечкина пещера в настоящее время является местом самого большого скопления одновременно зимующих летучих мышей *Myotis*. Описаны микроклиматические условия зимовок и их окрестностей с использованием инструментальных измерений температуры и влажности. Выявлены специфические предпочтения изученных видов, связанные с удаленностью зимующих групп относительно входов в пещеры и от подземных водоемов, специфических условий температуры и влажности. В результате мы получили предварительную оценку взаимосвязи между размером зимовок и благополучием популяций ночниц на территории Ленинградской области. Кроме того, мы попытались оценить уязвимость, как некоторых зимующих колони, так и популяций нескольких изученных видов в целом.

КЛЮЧЕВЫЕ СЛОВА: *Myotis*, зимовка, пещеры-штольни, температура, влажность, Россия.

Introduction

The bat fauna of the Leningrad Region is quite diverse compared to other regions of European Russia in similar latitudes. The reasons for that are both a considerable ingression of nemoral elements onto the boreal zone and the near maritime climate, and an ample supply of hibernacula. In general, eleven chiropteran species are known from the region (Airapety-

ants *et al.*, 1987), four of which are migratory, and seven hibernate at the same latitudes as their summer habitats. Five of them belongs to the Mouse-eared bats of genus *Myotis* Kaup, 1829: *Myotis dasycneme* (Boie, 1825) — pond myotis, *M. daubentonii* (Kuhl, 1817) — Daubenton's myotis, *M. nattereri* (Kuhl, 1817) — Natterer's myotis, *M. brandtii* Eversman, 1845 — Brandt's myotis, and *M. mystacinus* (Kuhl, 1817) — whiskered myotis. Mouse-eared bats preferred hibernacula are



Fig. 1. Entrance of the artificial Borshechkovskaya Cave (Leningrad Region, Luzhskii District, vicinity of Borshechovo Village (February, 2008). The Cave formed as a result of quartz sand mining for a Tarkovich Glass Manufacture.

caves or other underground shelters with similar conditions.

All mouse-eared bat species are unevenly distributed across the region, vary in abundance, and used different hibernacula. The distribution of massive aggregations of hibernating bats is directly associated with the locations of artificial caves (Strelkov, 1958; Il'in & Smirnov, 2000; Il'in *et al.*, 2003; Bogdarina, 2003; Kovalev *et al.*, 2014).

This paper is an overview and analysis of observations carried out in previous decades, including the author's own surveys from 2007–2015, covering the hibernacula of mouse-eared bats in artificial caves of the Leningrad Region, which is quite extensive on the European scale and quite distinct in terms of climate and biogeography.

The aim of the study was to identify patterns in the distribution and abundance dynamics of various mouse-eared bat species in underground hibernacula, and the effect of hibernation in artificial caves on the total size of the populations. Tasks of paper are: (a) counts of different mouse-eared bat species in all known artificial caves; (b) determining of the structural and microclimatic features of the hibernacula; (c) determining of the relations between the hibernacula and surrounding habitats; (d) preliminary estimation of a different values of

the inter- and intraspecies abundances; (e) risk estimation of hibernation period.

Material and methods

Bat's shelters. Bats of the studied region use caves, underground fortifications, wells and other artificial places, basements and attics of residential buildings for hibernate. Probably most caves of the Leningrad Region appeared as a result of quartz sand mining for a glass-making industry since the early 19th to the mid-20th century (Fig. 1). Some caves (e.g. Telezskije) appeared as result of the mining of quality artistic limestone. Limestone excavation formed abandoned artificial galleries of variable sizes, from 1 to 3 m in width, and 0.5 to 3 m in height, with some halls up to 15 m in diameter and 5–8 m of height. There are no natural caves in the Leningrad Region, apart from several small caverns worked by streams in steep river banks. Numerous old fortifications are presented on the Gulf of Finland shores and islands. Half of them are ruined or dilapidated.

Thus, annual counts were organized to regularly monitoring mouse-eared bat bats hibernating in artificial caves. During eight seasons from 2007 to 2015 we



Fig. 2. Map of the geographic position of the underground hibernacula of *Myotis* bats in the Leningrad Region. Also see Table 1.

surveyed about 35 artificial caves/cavities per year. The most significant and representative in information were hibernacula from follow group of caves: Sablinskije, Staroladozhskije, Borshchevskije, Rebrovskije, Korpovskije, and Telezskije (Fig. 2, Tab. 1).

All the caves were surveyed with making of detailed charts of 1:500 scale. The places with animals and its groups were mapped to avoid of undercounts and duplication of counts. Special detail studies with schema drawing (as example) have been performed for Tanechkina Cave. The schema is shown in Figure 2B. This cave is positioned on the steep left bank of the Volkhov River, and has two entrances 30 meters apart. These entrances facing to SW. One of them is located in the channel of the stream flowing into the Volkhov River. Another entrance is on the slope of this stream (Fig. 3). Tanechkina Cave appeared as result of the mining of quartz sands, and were abandoned over 150 years ago. The total length of all galleries over than 5500 m, the cave area about 10 720 m². The outline in plane is irregular oval; the greater length is about 200 m, width vary between 40 and 100 m. Underground lake seasonally fill from 45 to 60% of internal area of cave; its depth can reach 1.5 m. A stream about 1.5 km of length

fills the lake, and discharges entirely into the cave. Ceiling height from 0.7 to 2.6 m, and rising up to 5.5 m at scree areas. Originally, the ceiling height was even throughout the cave — 2.8 m, but the stream filled the volume with sand and reduced the height.

Records from seven years of surveys at the hibernacula include: 10 939 pond myotis, 2428 Daubenton's myotis, 1007 Natterer's myotis, 1009 Brandt's/whiskered myotis.

Shelters searching. Open source information from the Internet (see Appendix), archives of geological prospecting (unpublished data) and speleological publications (Khazanovich, 1982), and own surveys were applied to searching of entrances to artificial caves. There are quite many amateur 'cavers' in the region, who look for caves and, specifically, for new entrances. Given the present-day information availability it is safe to say that it is feasible to annually survey all currently known accessible underground cavities. Preliminary surveys have shown that *Myotis* bats hibernate in all the artificial caves and in some grottoes.

My own and other specialist researches have been directed to find of mouse-eared bats in other places, such as fortifications and old water conduits. Generally

Table 1. The geographic positions and physical characteristics of most known artificial caves and galleries of the Leningrad Region.

n	Caves*	Coordinates	Total length of galleries (m)
Group of Staroladozhskije Caves			
1	Tanechkina	N60°00' E032°18'	5500
2	Underneath church	N60°00' E032°27'	410
3	Plachushchaya grot	N60°00' E032°18'	15
4	Plachushchaya hole	N60°00' E032°18'	488
Group of Rebrovskije Caves			
5	Raschyoska	N60°30' E032°35'	240
6	Petrovskaya	N60°30' E032°35'	507
Group of Korpovskije Caves			
7	Korpovskaya	N58°42' E029°36'	400
Group of Rozhdestvenskije Caves			
8	Svyataya	N59°48' E029°57'	70
9	Grot	N59°48' E029°57'	11
Group of Borshevsckije Caves			
10	Kupol	N58°50' E030°21'	30
11	Goticheskaya	N58°50' E030°21'	420
12	Dvenadtsatistolbovaya	N58°50' E030°21'	390
Group of Yam-Tyosovo Caves			
13	Morovino	N58°53' E030°32'	10
Group of Telezskije Caves			
14	Petrovskaya	N59°41' E029°58'	360
15	Blizhnyaya	N59°41' E029°58'	20
16	Lesnaya 1	N59°41' E029°58'	30
17	Kolokol	N59°41' E029°58'	5
18	Gorelaya	N59°41' E029°58'	10
19	Zal Gigantov	N59°41' E029°58'	40
20	Tortsevaya	N59°41' E029°58'	50
21	Unnamed Cave (between Lesnaya 1 and Tortsevaya)	N59°41' E029°58'	30
22	Lesnaya 2	N59°41' E029°58'	90
23	Yashchera	N58°53' E029°50'	10
24	Dolgaya	N58°58' E028°58'	21
Group of Sablinskije Caves			
25	Levoberezhnaya	N59°40' E030°47'	6500
26	Grafskaya	N59°40' E030°48'	160
27	Zhemchuzhnaya	N59°40' E030°48'	550
28	Shtany	N59°40' E030°48'	1700
29	Veryovka	N59°39' E030°48'	800
30	Tryohglazka	N59°40' E030°47'	260
31	Lisja Nora 1	N59°39' E030°46'	17
32	Lisja Nora 2	N59°39' E030°46'	12
33	Lisja Nora 3	N59°39' E030°46'	79

Note: summarized data based on revised materials from the Russian Society for Speleological Research (<http://rosi-spelesto.narod.ru>).

these shelters did not contained bats. However some fortifications and water conduits were shelters for northern bat, *Eptesicus nilssonii* Keyserling et Blasius, 1839, and brown long-eared bat, *Plecotus auritus* (Linnaeus, 1758) (Chistyakov, 2004). Two specimens of Dauben-

ton's myotis were observed in underground ruins of Fort Ino on the Gulf of Finland Northern Coast (Chistyakov, 1999, 2009).

To spot of potential position of hibernacula in other shelters (wells, basements, attics), conducted surveys

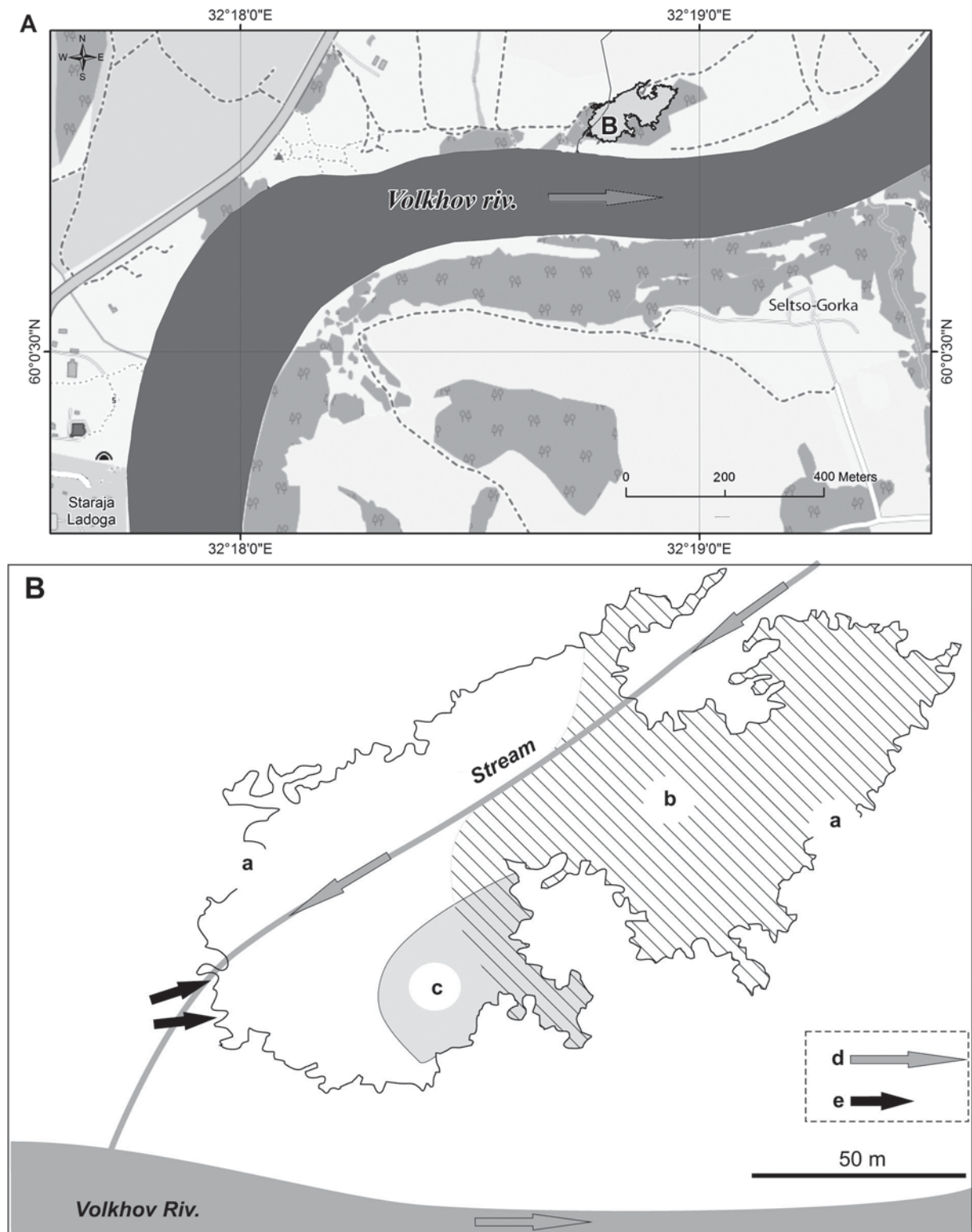


Fig. 3. Tanechkina Cave. A — map of the geographic position on the right bank of Volkhov River. B — plan of the Cave. Abbreviations: a — Cave outline; b — underground lake; c — pond myotis colony; d — stream direction; e — entrance.

among the residing peoples around known bat habitats, in addition we viewed media for searching information about that. A special information was announced on the website of the Interregional non-governmental organization “Centre for Nature Conservation Research and Initiative” (<http://naturconserv.org>). As a result, brown long-eared bat hibernacula was found in well near to the Yelizavetino Village, where dead bats were sometimes observed in buckets.

Precautions and some species identification. As is now known, frequent arousals during hibernation may exhaust or even kills bats. To avoid this we have tried to minimized influence, and did not touch the sleeping animals. As result we could not distinguish specimens of two morphologically similar species — Brandt’s myotis and whiskered myotis. Therefore, specimens probably belonging to one of these species were further defined as “Brandt’s/whiskered myotis”.

The attempt to differentiate between hibernacula of these two species was based on examination of the skulls extracted from carcasses retrieved from different caves, morphological traits of individuals and the general appearance of the aggregations.

After the large colony of Brandt’s/whiskered bats had been discovered in 2014, an attempt was made to find caves with hibernating whiskered myotis. Sixteen animals from large group in Telezskije caves were examined (10 ♂♂/6 ♀♀), and additionally four skulls from the same caves were inspected. Identification was based on three traits: baculum shape; tooth row measurements (premolar size, shape and position), color of the base of tragus (Kozhurina, 1997). All the inspected individuals were identified as Brandt’s myotis, and the skulls also belonged to this species. The generally uniform appearance of the animals in the dense aggregations suggests there were only Brandt’s myotis. As to bats in the eastward Staroladozhskije Caves, inspection of the skulls of three dead animals and examination of six individuals (3♂♂/4♀♀) for the three above-listed traits showed that these caves did not harbour whiskered myotis either. The artificial caves may, in fact, be inhabited by whiskered myotis, but checking all the animals for the species affiliation has no big sense while involving a risk of killing the animals (Strelkov & Buntova, 1982).

Population counts. Count of specimens of each hibernacula were performed from October to May. Each cave/cavity was examined from one to five times over a season. As a result of accountings it was found out that maximum population was reached in December. Analyses were performed by December’s count, because in this month was maximum abundance. Annual variation was studied using data of December–February. Hibernacula population is most stable in these months. Bats are more readily visible against level sand walls. The crevices where some animals hide in are usually quite shallow. Both individually located animals and the size of groupings (including per each defined species) were recorded.

Tools. Temperature and humidity were measured in addition to animal counts. We used thermohygrometers RST 06018 (Sweden, China). In additions, in some cases we described elevation of specimen groups relatively of floor level, type of surface where the animals located (wall, ceiling), and using of micro-shelters (crevices, niches) or open space of surfaces. All measurements were performed with using tape-line. Biotopes around the hibernacula were surveyed for bat presence before the winter season (till the start of bats hibernation). We used special bat detector — Pettersson Elektronik D-200 (Sweden) that allowed to estimates of summer count and abundance in specific places (results were published, see details in Kovalyov & Popov, 2011; Kovalyov & Shchekhovskiy, 2014).

Results

Pond myotis. Specimens of this species were found in 13 caves out of 35 studied. In two of them pond myotis hibernated annually. Around 99% of all pond myotis in the study area hibernated in Tanechkina Cave of the Staroladozhskije Caves group (Tab. 2). Another studied caves and caverns with occasional meeting of pond myotis were situated either close to Tanechkina Cave or not so far from the bats’ summer habitats (Tab. 2). According to information from other regions, the pond myotis is more depending on temperature and humidity conditions through the hibernate period, than other bat species. The timeframe for the stay of pond bats in Tanechkina Cave is from late September to late May. Animals may keep entering the cave until late November and begin to emerge from the Cave in the first third of March (Kovalyov & Popov, 2011).

The pond myotis colony occupies only part of Tanechkina Cave. It has a discrete location, and the core of the colony occupy about 1600 m² (Fig. 3B). The temperature/humidity conditions of Tanechkina Cave have changed somewhat since the 1950s. According to Strelkov (1958), the temperature in this cave ranged +5 to +7°C, and air humidity was about 95% or higher. At present, the temperature that measured about 30 m from entrance is ranged +10 to +12 °C during period from November to May, and pond myotis here hibernate at this temperature conditions. This temperature interval is much higher than the optimum for this species that described for Samarskaya Luka Dungeons (Smirnov *et al.*, 2008). About 25% of individuals lodge on the walls and ceiling above underground lake surface, another part of colony lodge very close to water. About 5% of the individuals or their groups (before 50 bats) are placed outside the core of the colony in more remoted parts of the cave. Within the core the pond myotis are kept apart, and formed either small groups not more than 10 animals, or more large compact aggregations of up to 90 animals. These observations are consistent with results of Smirnov *et al.* (2012) for Mount Popov’s artificial caves of Samarskaya Luka, where pond myotis showed a high degree of uneven distribution. Specif-

Table 2. Results of annual counts of pond myotis in caves of the Leningrad Region during period 2008–2015.

n	Caves	2008	2009	2010	2011	2012	2013	2014	2015
1	Staraya Ladoga, Tanechkina	934	1228	1297	1784	1180	1922	1168	1301
2	Staraya Ladoga, Plachushchaya grot	1	0	–	–	1	0	2	2
3	Staraya Ladoga, Plachushchaya hole	–	–	–	–	10	8	–	–
4	Korповskaya	6	6	4	3	2	2	2	0
5	Borshchevo, Dvenadtsatistolbovaya	7	0	0	0	0	0	0	0
6	Yam-Tyosovo, Morovino	1	0	0	0	0	0	0	0
7	Telezi, Petrovskaya	0	1	0	0	0	–	5	–
8	Telezi, Zal Gigantov	–	–	–	–	–	–	5	0
9	Telezi, Tortsevaya	–	–	–	–	–	–	4	0
10	Telezi, Lesnaya 2	–	–	–	–	–	–	18	1
11	Sablino, Zhemchuzhnaya	0	0	0	–	0	–	6	1
12	Sablino, Levoberezhnaya	1	6	0	–	3	–	4	2
13	Sablino, Shtany	–	1	–	–	0	2	3	1
14	Sablino, Lisja nora 1	–	0	–	–	2	–	0	0
15	Sablino, Lisja nora 2	–	0	–	–	1	–	–	–
16	Sablino, Lisja nora 3	–	2	–	–	0	–	0	0

Note: “–” — no data; “0” — bats not found.

ic characters of the local distributions of this species are occupation of open surface; if some of the biggest aggregations occupy shallow crevices, then all individuals have access to the open space of the cave. In addition, during hibernation season animals occasionally can change personal location, and these rearrangements lead to some alterations of group's size.

The studied hibernating colonies (hibernaculi) were described with using two parameters: number of groups and their size (number of animals in each group). The relatively distribution of individuals among groups proved to be quite accurately described by the power function with negative fractional exponent. The approximation confidence factor (R^2) was near one. This was a typical distribution in any cases when the number of individuals in the cave was between 500 and 1900 (Fig. 4A,B).

Six size classes can be allocated for pond myotis that hibernating in large colonies. Each of classes differs in attachment possibilities, thermoregulation ability, and sex-age characteristics. These classes are: single animals; pairs; small groups from 3 to 10 individuals (each animals of single–small group has lateral contact with environments); middle-sized group from 11 to 30 individuals, where part of them surrounding the group, and where they do not have problems with the attachments; large group from 31 to 50 individuals, where animals have some problems with the attachments on

the flat surfaces of walls and ceiling; very large group with more than 50 individuals, forming with exclusive attachment options, often located in crevices.

The ratio of groups of different size in the hibernaculum was more constant than the ratio of individuals belonging to these categories. The shares of single individuals and pairs usually remained constant. The most numerous size classes were single individuals, and small groups with 3 to 10 individuals. Each of the three classes with 3–50 animals (small–middle–large) was represented by a relatively stable number of hibernating bats, roughly a third of its total abundance. In years of maximum of population, groups bigger than 50 individuals appear, and the number of individuals hibernating in groups increased from 11 to 30.

Examination of the 30 single individuals showed that males slightly dominate in numbers ($18\sigma^{\sigma}/12\phi^{\phi}$). Four groups with 2, 6, 13, 35, correspondingly, showed nearly equal proportion of males and females number (total examination $27\sigma^{\sigma}/29\phi^{\phi}$). The group distribution structure during hibernate and during emergence of pond myotis from the cave varied less significantly compared to variations among years, and was not related to abundance. Thus, although grouping structure does not show whether the hibernaculum has reached its maximum, one can still estimate the abundance in the hibernaculum without doing a full census.

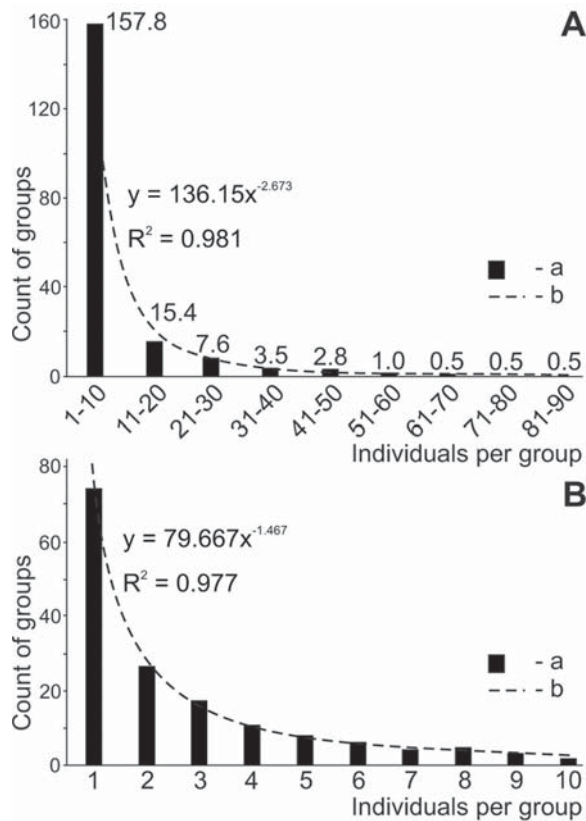


Fig. 4. The distribution of the mean number of pond myotis groupings of different size (A); and groupings with comprising from 1 to 10 animals (B). Total count of animals ranged 500 to 1900 animals (nine repeats of abundance estimation). Abbreviations: a — counts of groups; b — the power function (see detail in text).

Numbers of pond myotis that were found in Tanechkina Cave (Fig. 5), as the preferred species habitat, have increased considerably since the 1950s (Fig. 6). The abundance has doubled also in the years of our surveys (Fig. 7A). It is noteworthy that after the abundance threshold in the Tanechkina Cave had been approached, the number of hibernating bats the next year dropped to around 1200. High abundance years were also noted for an early (March) beginning of emergence of a considerable part of bats from the cave. At the same time, the number of dead bodies found during emergence was also high (up to 60).

Summer habitats of pond myotis are situated 150 km or more from the hibernaculum in Tanechkina Cave (see details in Kovalyov & Popov, 2011). No pond myotis have been observed around the key hibernaculum from May to September. A few bats were registered within the audible range of the detector (80 m) not far from the cave in October, before they entered the hibernaculum. The rest of the caves where the pond myotis was found to hibernate were situated either in the same area as summer habitats or along autumn migration routes (Kovalyov & Popov, 2011; Kovalyov, 2011).



Fig. 5. Group of pond myotis in the Tanechkina Cave (January, 2011). © I. Popov 2008.

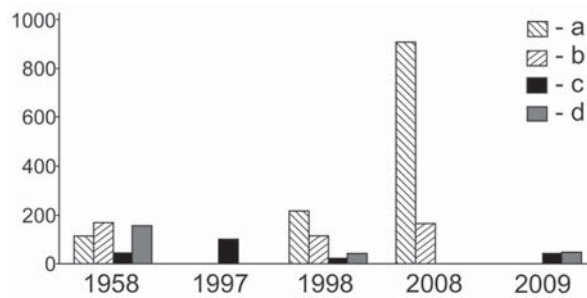


Fig. 6. Results of the estimation of the number of the different species of *Myotis* bats within caves of the Leningrad Region during last 60 years according to published data (Strelkov, 1958; Iljinsky *et al.*, 1998; Chistyakov *et al.*, 1999; Kovalyov & Popov, 2011). Abbreviations: a — pond myotis (Tanechkina Cave); b — Daubenton's myotis (Tanechkina Cave); c — Natterer's myotis (Levoberezhnaya Cave); d — Brandt's/whiskered myotis (Staroladozhskije and Sablinskije Caves).

Daubenton's myotis. Specimens of this species were found in 16 caves out of the 35, and were present in ten caves at each estimation of abundance during 2008–2015 (Tab. 3). On average, around 70% of all hibernating animals of this species were found in Tanechkina Cave. The rest 30% were distributed quite evenly among all major groups of caves (except Telezskije Caves). Hibernaculum conditions in Tanechkina Cave were described above. Daubenton's myotis were evenly scattered throughout the cave from the entrance, where the temperature on frosty days was near 0°C, to the farthest premises. Up to 80% of the single animals occupy the open surface of walls and ceiling above dry floor either open water of underground lake. Another 20% of the animals formed groups from 2 to 5, and occasionally specimens Daubenton's myotis were detected within groups of pond myotis. This ratio (80/20) here remained stable during several years. In other caves Daubenton's myotis were also mostly staying individually. A similar single distribution of this species was observed in the Samarskaya Luka Dungeons.

The microclimate conditions in different known Daubenton's myotis hibernaculum varied widely: temperature ranged from 1 to 12°C, humidity from 70% to

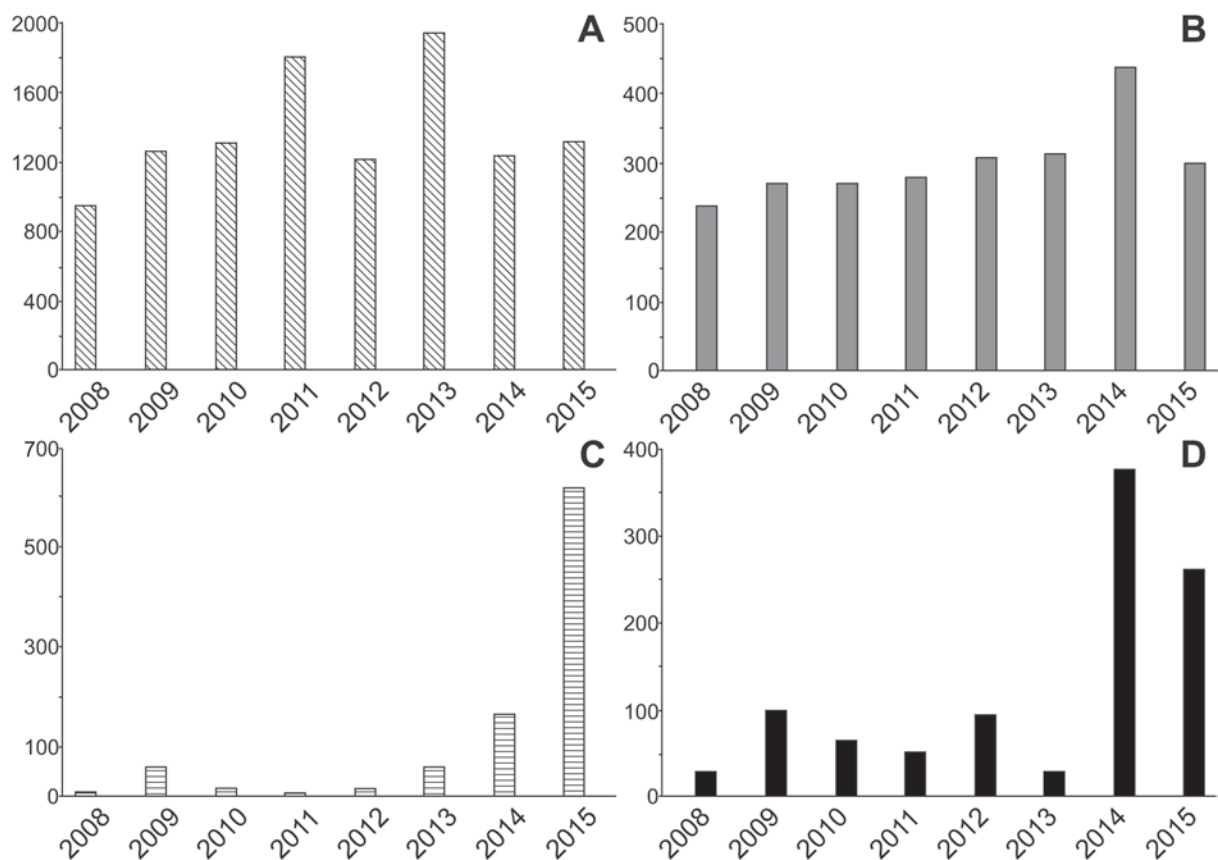


Fig. 7. Total number of individuals of the different species of *Myotis* bats counted in caves of the Leningrad Region during period 2008–2015. A — pond myotis, B — Daubenton's myotis, C — Natterer's myotis, D — Brandt's/whiskered myotis. Abbreviations: OX — years; OY — number of animals.

Table 3. Results of annual counts of Daubenton's myotis in caves of the Leningrad Region during period 2008–2015.

n	Caves	2008	2009	2010	2011	2012	2013	2014	2015
1	Staraya Ladoga, Tanechkina	165	189	219	199	199	218	302	189
2	Staraya Ladoga, Underneath church	5	10	9	11	6	6	14	–
3	Staraya Ladoga, Plachushchaya grot	0	0	–	–	1	1	2	–
4	Staraya Ladoga, Plachushchaya nora	–	–	–	–	27	24	0	–
5	Rebrovskaya, Raschyoska	7	12	–	18	9	6	12	–
6	Rebrovskaya, Petrovskaya	14	5	–	19	4	18	41	–
7	Korpovskaya	30	26	28	27	26	17	20	–
8	Rozhdestveno, Grot	0	1	–	–	1	–	0	–
9	Borshchevo, Goticheskaya	9	8	10	4	10	11	27	13
10	Borshchevo, Dvenadtsatistolbovaya	2	2	6	4	6	4	6	8
11	Telezi, Tortsevaya	–	–	–	–	–	–	1	2
12	Dolgaya	0	1	–	–	1	–	0	–
13	Sablino, Levoberezhnaya	3	5	1	–	18	–	13	70
14	Sablino, Zhemchuzhnaya	1	7	–	–	1	4	–	6
15	Sablino, Shtany	–	2	–	–	1	6	1	12
16	Sablino, Lisja nora 3	–	3	–	–	0	–	0	2

Note: see in Table 2.

100%. On some occasions, Daubenton's myotis hibernated within groups of northern bat, when the temperature temporarily dropped below 0° C, and no other bat species were present. For instance, they were found in Dolgaya Cave and Fort Ino (Chistyakov, 2009).

From the 1950s to 2008 the Daubenton's myotis abundance at most hibernacula in the Leningrad Region has apparently remained fairly constant. A noteworthy fact however is a substantial reduction in their numbers in the group of Sablinskije Caves (Fig. 6). The abundance of Daubenton's myotis in Tanechkina Cave, as the preferred species habitat, was slightly increasing (Fig. 6). An upward trend in the abundance of it has been observed during the period of this study in all caves. The rise was especially significant in 2014 (Fig. 7B).

The summer habitats of Daubenton's bats are situated around most of the caves with their hibernacula (as observed by the author).

Natterer's myotis. Specimens of this bat were found in 11 caves out of the 35, and were present in three caves at each estimation of abundance during 2008–2015 (Tab. 4). Compare to another species, hibernating specimens of Natterer's myotis were observed only in two groups of caves — Telezskije and Sablinskije. Around 90% of the animals were found in Sablinskije Caves (mainly in Levoberezhnaya). Levoberezhnaya

Cave characterized by the following environmental conditions: temperature ranged from 8 to 12°C; humidity from 74 to 100%. Natterer's myotis there hibernated under two types of conditions depending on the distance from the entrance: 60% of individuals hibernating in distance from 20 to 100 m from entrance were exposed to a temperature of 8 to 10°C and humidity of 74 to 93%; another 40% than hibernating in distance from further than 100 m from one were exposed to a temperature of 10 to 12°C and humidity of 90 to 100%. The most Natterer's myotis hibernated in crevices above dry areas of the Cave. A part of individuals occupied open flat surfaces of walls and ceiling, and often above open water; many animals were hanging on a wet ceiling with dripping water (either in deep horizontal crevices or openly). A lighted tourist path was set up in the first part of the cave, whereas no visitors were allowed into the second part. Around 70% of the animals stayed individually, up to 20% roosted in pairs, the biggest groupings comprised 4 individuals. Only in 2015, after a significant increase number Natterer's myotis was observed five groups of more than 10 individuals (11–24). In Telezskije Caves and the similar Lisja Nora-3 Cave Natterer's myotis hibernated at a temperature of 4 to 6°C and humidity of 60 to 75%.

The Natterer's myotis abundance at hibernacula in the Leningrad Region has fluctuated between the 1950s

Table 4. Results of annual counts of Natterer's myotis in caves of the Leningrad Region during period 2008–2015.

n	Caves	2008	2009	2010	2011	2012	2013	2014	2015
1	Telezi, Petrovskaya	0	3	–	3	0	–	6	–
2	Telezi, Blizhnaya	0	0	–	1	0	–	–	4
3	Telezi, Proval	0	4	–	–	0	–	–	–
4	Telezi, Lesnaya 1	–	0	–	–	1	–	3	–
5	Telezi, Zal Gigantov	–	–	–	–	–	–	3	–
6	Telezi, Tortsevaya	–	–	–	–	–	–	3	3
7	Telezi, Lesnaya 2	–	–	–	–	–	–	5	3
8	Sablino, Levoberezhnaya	9	43	17	–	106	–	124	503
9	Sablino, Zhemchuzhnaya	–	5	–	–	6	5	8	56
10	Sablino, Shtany	–	4	–	–	7	12	10	46
11	Sablino, Lisja nora 3	–	0	–	–	0	–	4	–

Note: see in Table 2.

and 2009, yet remaining at about the same level. The most complete data have been gathered for Levoberezhnaya Cave of the group of Sablinskije Caves. The highest abundance there was recorded in 1997, before the tourist route was opened, and the number of the animals decreased dramatically in the following year (Fig. 6). During the study period, the Natterer's myotis abundance has been slightly growing in all caves. Comparable data were obtained in 2009, 2012, 2014 and 2015, and no surveys were carried out in Levoberezhnaya Cave in other years (Fig. 7C).

Brandt's/whiskered myotis. Specimens of this species complex were found in 22 caves out of the 35, and were present in three caves at each estimation of abundance during 2008–2015, and observed in all groups of caves (Tab. 5). Prior to 2014, around 50% were recorded from Staroladozhskije Caves, and about 25% in each of Sablinskije and Telezskije caves. In 2014, 75% of all the animals were found in Telezskije Caves. The reason for the change was the discovery of four new entrances to Telezskije Caves, where major aggregations of the bats were situated. Non-professional cavers encountered bats every time they discovered a new entrance. Hence, bats must have been able to get into the caves through small openings unsuited for humans. In all the caves Brandt's/whiskered myotis hibernated not far from entrances at a temperature of 3 to 6°C, and humidity of 60 to 80%. Where the colony was small in size, Brandt's/whiskered myotis were attached individually. If a cave contained more than 20 bats, part of the animals clumped together in groups of up to 10. Where abundances were higher, the animals formed large dense aggregations of up to 50 individuals. Single individuals and small groups preferred secretive locations, in crevices or on small benches, and rarely stayed on open flat surfaces. Larger aggregations chose to stay openly.

Brandt's/whiskered myotis preferred dry conditions in a hibernaculum, and hardly ever hibernated above water.

Brandt's/whiskered myotis abundance at hibernacula in Staroladozhskije and Sablinskije caves had declined from the 1950s to 2009 (Fig. 6). During the study period until 2014 the average abundance remained quite constant, with a decline in Staroladozhskije and an insignificant rise in Sablinskije Caves. Comparable data for Staroladozhskije and Sablinskije caves were obtained in 2009, 2012, 2014 and 2015, since in other years Levoberezhnaya Cave was not surveyed. The large Brandt's/whiskered myotis colony newly discovered in Telezskije Caves in 2014, 2015 yielded a 3.5-fold increase in the species abundance at the hibernacula (Fig. 7D).

Discussion

The analysis of the distribution of mouse-eared bats among hibernacula showed that the Natterer's myotis, pond myotis, and complex Brandt's/whiskered myotis had 2–3 constantly preferred caves, although minor numbers of individuals of these species may in some years be distributed quite widely. Daubenton's myotis were less strictly attached to specific shelters, hibernating in all groups of caves over years. Noteworthy is the greater number of caves with non-annual hibernacula of Brandt's/whiskered myotis as compared to other species. This may indirectly point to the hibernation of both species there: Brandt's myotis and whiskered myotis (Tab. 7A).

Previously available information and the our results show that caves and artificial caves are by far the only hibernation habitat for the pond myotis under the climatic conditions of its Russian distribution range (Strelk-

Table 5. Results of annual counts of Brandt's/whiskered myotis in caves of the Leningrad Region during period 2008–2015.

n	Caves	2008	2009	2010	2011	2012	2013	2014	2015
1	Staraya Ladoga, Tanechkina	22	20	51	41	40	18	16	39
2	Staraya Ladoga, Plachushchaya grot	4	0	–	–	1	0	0	0
3	Staraya Ladoga, Plachushchaya hole	–	–	–	–	0	3	0	0
4	Rebrovskaya, Raschyoska	0	5	–	0	0	1	1	0
5	Rebrovskaya, Petrovskaya	0	3	–	0	0	1	6	0
6	Korpovskaya	1	6	3	2	1	0	0	–
7	Rozhdestveno, Svyataya	0	1	–	–	0	–	0	0
8	Borshchevo, Goticheskaya	2	0	0	0	1	2	1	1
9	Borshchevo, Dvenadtsatistolbovaya	0	0	0	1	1	0	0	0
10	Telezi, Petrovskaya	1	8	2	3	1	–	6	–
11	Telezi, Blizhnaya	0	22	0	5	1	–	–	2
12	Telezi, Lesnaya 1	–	8	2	–	6	–	10	–
13	Telezi, Kolokol	–	–	1	0	–	–	–	–
14	Telezi, 5	–	–	–	–	2	–	–	1
15	Telezi, Zal Gigantov	–	–	–	–	–	–	120	–
16	Telezi, Tortsevaya	–	–	–	–	–	–	44	35
17	Telezi, Telezi + (between Tortsevaya and Lesnaya 2)	–	–	–	–	–	–	4	2
18	Telezi, Lesnaya 2	–	–	–	–	–	–	105	82
19	Sablino, Levoberezhnaya	0	21	6	–	40	–	48	68
20	Sablino, Zhemchuzhnaya	–	3	–	–	1	1	2	14
21	Sablino, Shtany	–	2	–	–	0	4	8	18
22	Sablino, Lisja Nora 3	–	0	–	–	0	–	5	–

Note: see in Table 2.

ov, 1958, 1971a,b; Orlov, 1998, 1999; Kovalyov & Popov, 2011). It is safe to say that the number of pond myotis hibernating in Tanechkina Cave is directly related to their abundance in the region. This becomes obvious when comparing their abundances in summer and winter habitats, given the limited availability of such habitats (Kovalyov & Popov, 2011). The rise in the number of pond myotis counted at the hibernaculum in 2011 and 2013 was in line with an expansion of the summer range into the southern part of the Karelian Isthmus and expansion of the autumn aggregation on the northern coast of Finland Gulf to Kieper Ort Peninsula (Kovalyov, 2012). Early in the 2000s pond myotis first appeared (Siivonen & Wermundsen, 2003) and a few individuals were found at hibernacula of the Southern Finland. These findings evidence an expansion of the species range within the region as result of a rising abundance of population core. At the same time when

the number of wintering animals of the Tanechkina Cave reached 2000, the following year the number decreased to 1200 individuals. We believe the reasons are both the hibernaculum capacity and the availability of summer habitats suitable for spring migrations (Kovalyov & Popov, 2011).

Table 6. Records of *Myotis* bats in caves during all previous studies (A), and period of our monitoring 2008–2015 (B).

Species	A	B
Pond myotis	13	2
Daubenton's myotis	16	10
Natterer's myotis	11	3
Brandt's/whiskered myotis	22	3

Table 7. Characteristics of the *Myotis* bats wintering in caves of Leningrad Region.

Species	T, °C	Humidity, %	Distance from the entrance, m	Preferred aggregation, individuals	Surface location	Presence in surrounding habitats	Part of the Region
Pond myotis	10–12	90–100	> 20	10–50	openly, in crevices	absent	Eastern
Daubenton's myotis	1–12	70–100	10 to 200	1–2	openly	present	Eastern, Central, Western
Natterer's myotis	4–12	60–100	5 to 200	1–2	openly, in crevices	vary	Central
Brandt's/whiskered myotis	3–6	70–80	5 to 20	2–5	openly, in crevices	vary	Western

The fact that there were no known pond myotis colonies bigger than 1000 individuals (Kuz'yakin, 1950; Strelkov, 1958; Masing, 1990; Orlov, 1999; Limpens *et al.*, 1999; Limpens *et al.*, 2000) suggests that the species is generally unlikely to form bigger colonies. Given that the distribution into groups at the hibernaculum in this cave is modeled by the power function, one can say that the group structure of the colony conforms to fractal laws, meaning that when the abundances rises, a self-similar structure is reproduced, where groups of 100 or more animals appear. This group size is limited by attachment possibilities, and obviously affects the hibernation success of individual animals in a large grouping. The fractal structure must also be a significant factor in the thermoregulation of all bats in the hibernaculum. By moving within and among groups of different size during the hibernation period bats maintain the temperature regime needed for a physiologically optimal hibernation. The high mortality found in the cave in the spring following abundance maximums is indirect evidence of ill-being in the hibernaculum. The chance of epidemics and other force majeure causes of high mortality among bats hibernating in a little visited cave is low.

Although the pond myotis has a wide distribution from Belgium to Northern Kazakhstan, the northern limit of its range running at around N 60°, individual specimens are marked up to N 64°, and the southern limit from N 44° to 50° (Kozhurina, 2009), the range is discontinuous, apparently due to concentration around massive hibernation areas (Strelkov, 1970; Limpens *et al.*, 2000). One can thus speak of optimal pond myotis abundance in the region at 1600–1800 individuals, which has been reached, and the species started dispersing to other parts of the range. The main range expansion trend associated with the Tanechkina Cave hibernaculum is towards the south of the Karelian Isthmus and Southern Finland, as well as eastwards from the St. Petersburg – Luga line. The trend has been exhausted by now, as all suitable summer habitats have been

occupied. Longer-range dispersals are apparently directed south-westwards, towards the Pskov Region and Estonia.

The number of Daubenton's myotis at hibernacula depends on the size of the cave. This correlation is broken only in the caves with no habitats in the surroundings (Telezskije Caves), or where the nuisance factor exceeds the acceptable threshold (most of Sablinskije Caves). In most caves Daubenton's myotis appear to arrive from the surrounding summer habitats. The exception is Tanechkina Cave. The number of animals in this cave considerably exceeds the capacity of the nearby biotopes, populated by two individuals per 1 km of river or up to 10 individuals per 1 km² of waterbody (unpublished data). This cave gathers Daubenton's myotis from an at least 50 km radius.

Absolute abundances of Daubenton's myotis in the Leningrad Region cannot be directly estimated by counts at hibernacula in artificial caves. The temperature and humidity at which Daubenton's myotis hibernate in the caves range widely, the temperature sometimes being at zero. Hence, the species may stay in various shelters other than caves. The number of individuals in caves can however be a good indicator of the population abundance. Summer counts of Daubenton's myotis using geographical information analysis of suitable habitats in the region have estimated the species abundance at 4000–4500 individuals (Kovalyov & Shchekhovskiy, 2014). Thus, around 10% of the regional population that hibernates in caves.

For the Natterer's myotis this region is the north-eastern limit of its distribution range (Kozhurina, 2009). Presence in only two groups of caves, microclimate preferences at hibernacula, steadily low rate of abundance growth after the establishment of favorable conditions in Levoberezhnaya Cave suggest with high probability that Natterer's myotis in the Leningrad Region chiefly hibernate in caves. Hence, their population in the region is fairly small, no more than 1000 individuals. Summer counts of the animals using bat detectors

revealed only singular Natterer's myotis individuals, confirming their low abundance.

Unusually high increment of number of Natterer's myotis in the group of Sablinskije Caves in 2015 may be due to the fact that in the period 2014–2015, the most of Telezskije Caves were destroyed during the construction of the highway Saint-Petersburg – Tallinn. The movements of Natterer's myotis could be caused by destruction of the wintering places. Probably, they lived in those of Telezskije Caves which were destroyed during a roadwork and were not earlier examined because of inaccessibility for humans. But perhaps it is a natural process of resettlement from the Baltic States.

The hibernaculum in Telezskije Caves appears to be the key winter habitat of the Brandt's/whiskered myotis in the region. Given the limited amount of summer habitats, one can presume the species abundance in the region to be characterized by the number of individuals at hibernacula. According to some data, the area of underground cavities in Telezskije Caves yet closed to people is less than 25% of known spaces. Assuming that bats can reach these areas, inaccessible to people, the total abundance of the Brandt's myotis in Telezi Caves may be higher than in the counts, probably amounting to 600–700 animals. The size of the compact aggregations, up to 50 animals, indirectly evidences that more bats than counted hibernate in Telezi.

It is possible to estimate the Brandt's/whiskered myotis abundance relying on counts at hibernacula, in spite of the low temperature conditions they choose to stay at in caves. For instance, the noticeable decline since the 1950s in Staroladozhskije and Sablinskije caves must have been a direct consequence of the removal of many Brandt's Myotis from the caves, when only females (60 individuals) were sampled to be checked for pregnancy (Strelkov, 1971a). The fact that the Brandt's myotis has not recovered its former numbers in these caves even after 40 years suggests that the species abundance in the Leningrad Region is low and that there are no other hibernacula in the region. Which means that the total counts of the Brandt's myotis regional population is about 1000 animals. The Brandt's myotis is one of the most long-living bat species: the average life span being 15–20 years, some individuals may live up to 38 (Khritankov & Ovodov, 2001). Given their longevity and low fecundity, the significance of each individual for the well-being of the population is very high. Decrease in number of Brandt's myotis in 2015 in Telezskije Caves is bound to destruction of their most part at construction of the highway Saint-Petersburg–Tallinn. During this period, almost 2 times was increased the number of Brandt's myotis in Sablinskije Caves. Perhaps this is due to the movement of bats from broken Telezskije Caves.

Species preferences for hibernacula in *Myotis* bats. Comparing analyses of the hibernaculum preferences of the different *Myotis* bat species were revealed that the strictest demands for conditions at the hiber-

naculum demonstrated by pond myotis. Natterer's myotis accept a relatively wide range of temperature and humidity conditions, yet within certain limits that within studied region are inherent only to caves. Brandt's/whiskered myotis choose the coldest and least humid sites in caves, but require that these conditions remain stable. Daubenton's myotis hibernate at the most diverse conditions, caves not being their only habitats. Hibernation characteristics of the whiskered myotis cannot be judged by data from artificial caves, since only occasional individuals have been found there, and the species seems to prefer different winter shelters (Tab. 7).

Considering the numbers of animals at hibernacula and assessing the role of artificial caves in the life cycle of different species, one can say that pond myotis are rather vulnerable in spite of the relatively high abundance and steady growth of its population, because they are completely dependent on the state of a single cave. The most threatening is the situation for the Natterer's myotis and the Brandt's/whiskered myotis. Their abundances are low, and they are highly vulnerable in all winter habitats because they are prefers only one or two known caves. The species of least concern is the Daubenton's myotis, which hibernates in most of the caves and employs the widest range of microclimatic conditions. The vulnerability of the whiskered myotis cannot be determined relying on data from the hibernacula, at least in our study. In general, the anthropogenic factor positively influences hibernacula of bats as factor forming of shelters. The artificial caves and various buildings create the favorable conditions for expansion of areas of bats habitat and allow to reach high concentration on winterings (Ilyin *et al.*, 2003; Chistiakov & Nikulin, 2010). However, the shortcomings of the protection measures in large concentrations of bats can lead to the death of a large number of animals (Mitchell-Jones *et al.*, 2007; Wermundsen, 2010; Kovalyov *et al.*, 2012).

Conclusions

Studying of the *Myotis* bats hibernacula places in Leningrad Region applied to the following conclusions. Microclimate characteristics of the hibernacula are highly diverse, from 3 to 12°C, and humidity from 60 to 100%. These conditions are species-specific. The most stenobiotic species is the pond myotis, and the species least demanding towards the hibernaculum conditions is the Daubenton's myotis. In addition, large hibernacula of pond myotis were found in Tanechkina Cave of the group of Staroladozhskije Caves; Natterer's myotis in Levoberezhnaya Cave of the group of Sablinskije Caves; Brandt's/whiskered myotis in Telezskije Caves; Daubenton's myotis in Tanechkina Cave and a few small caves, namely Korpovskaya, Rebrovskije, Borshchevskije. The number of pond myotis counted at the hibernacula ranged between 1600 and 1800 individuals, and quite accurately portrays the size of the region-

al population; Daubenton's myotis counts at hibernacula account for around 10% of the regional population that estimates as 4000–4500 animals; the number of Natterer's myotis at hibernacula approximately correspond to their total regional population abundance that is less than 1000 individuals; the Brandt's/whiskered myotis is apparently somewhat more abundant in the region than what was maximally recorded from caves, since not all bat-inhabited underground structures are accessible, and the species population in the region is about 1000 animals; most of them do not hibernate in caves, and their total abundance is unknown, but appears to be very low.

Hibernating pond myotis are vulnerable because they massively concentrate only in one known cave (99% in Tanechkina Cave). The most vulnerable species in the region are the Brandt's myotis and the Natterer's myotis because of low abundance and aggregation in several risk-exposed caves. The whiskered myotis in the region is vulnerable because of low abundance. The Daubenton's myotis is in the most secure situation.

ACKNOWLEDGEMENTS. The author is grateful to all those who have taken part in collecting data on bat hibernacula in different years: M.G. Noskova, I.Yu. Popov, N.N. Irashin, E.A. Shchekhovskiy, A.D. Loginov, E.V. Palenova.

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Appendix. List of internet-sources used for searching of caves and grottoes within territory of the Leningrad Region.

- Web-resource "NATUREworld", <http://natureworld.ru>;
- Web-page of the Russian Society of Speleological Research "Speleology", <http://rosi-spelesto.narod.ru>;
- Web-resource "Underground Speleological Portal of the Sablinskije Caves", <http://sablino.narod.ru>;
- Web-resource "caves.ru", <http://www.caves.ru>.