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Parasites of *Myotis brandtii* and *M. daubentonii* (Chiroptera: Vespertilionidae) in the north of the range (Karelia, Russia)

Daria I. Lebedeva, Vladimir V. Belkin, Maria K. Stanyukovich†, Andrey N. Lyapunov & Sergey V. Bugmyrin*

ABSTRACT. In this study we report new data on the parasites of two bat species, *Myotis brandtii* and *Myotis daubentonii*, in the north of their distribution. The parasitological surveys were carried out in the middle taiga subzone of Karelia (Northwestern Russia) in July and August 2020. Altogether, 16 parasite species were recorded: eight helminths (Trematoda — 5; Cestoda — 1; Nematoda — 2) and eight ectoparasites (Arachnida: Sarcoptiformes — 1, Mesostigmata — 2 Trombidiformes — 1; Insecta: Siphonaptera — 2 and Diptera — 2). *Myotis daubentonii* hosted eleven parasite species, whereas *M. brandtii* hosted eight species. The parasite fauna of both species mostly consisted of widely distributed specialist taxa. The species found for the first time in Karelia were *Prosthodendrium ascidia, Parabascus duboisi, Vampirolepis balsaci, Molinostrongylus spasskii, Pterygodermatites bovieri, Macronyssus diversipilis, Spinturnix myotis, Nycteribia kolenatii, Penicillidia monoceros*, *Ischnopsyllus* (*I.*) *mysticus* and *Myodopsylla trisellis*. Encysted gravid females of mites *Nycteridocoptes poppei* (Sarcoptiformes) were found on the patagium of *M. daubentonii*. This is the northernmost record of this parasite in the Palearctic. We obtained partial *cox1* mitochondrial DNA sequences for *N. poppei*, providing the first genetic data for this genus.

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Паразиты *Myotis brandtii* and *M. daubentonii* (Chiroptera: Vespertilionidae) на севере ареала (Карелия, Россия)

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РЕЗЮМЕ. Представлены новые данные о паразитах двух видов летучих мышей: *Myotis brandtii* и *Myotis daubentonii*, на севере их ареала. Паразитологические исследования проводились в среднетаёжной подзоне Карелии (северо-запад РФ) в июле и августе 2020 года. Всего было зарегистрировано 16 видов паразитов, из которых восемь гельминтов (Trematoda — 5; Cestoda — 1; Nematoda — 2) и восемь эктопаразитов (Arachnida: Sarcoptiformes — 1, Mesostigmata — 2 Trombidiformes — 1; Insecta: Siphonaptera — 2 и Diptera — 2). У *Myotis daubentonii* отмечено 11, у *M. brandtii* — 8 видов паразитов. Паразитофауна обоих видов состояла из широко распространенных специализированных видов. Впервые в Карелии были обнаружены: *Prosthodendrium ascidia, Parabascus duboisi, Vampirolepis balsaci, Molinostrongylus spasskii, Pterygodermatites bovieri, Macronyssus diversipilis, Spinturnix myotis, Nycteribia kolenatii, Penicillidia monoceros, Ischnopsyllus (I.) mysticus и Myodopsylla trisellis*. На патагиуме *M. daubentonii* были отмечены инкапсулированные самки *Nycteridocoptes poppei* (Sarcoptiformes). Это самая северная находка этого паразита в Палеарктике. Мы получили ча-

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стичные последовательности митохондриальной ДНК *cox1* для клещей *N. poppei*, представив первые генетические данные для этого рода.

КЛЮЧЕВЫЕ СЛОВА: ночница Брандта, водяная ночница, гельминты; гамазовые клещи, блохи, *Nycteridocoptes*, таежная зона.

Introduction

Bats (Chiroptera, Vespertilionidae) are numerous and diverse mammals distributed almost ubiquitously except Antarctica and Polar regions (Simmons, 2005). One of the northernmost areas of their distribution is Fennoscandia, which includes the Scandinavian Peninsula, the Kola Peninsula, mainland Finland and Karelia. The species diversity and population abundance of bats in Fennoscandia used to be low (Siivonen & Sulkava, 1999; Siivonen & Wermundsen, 2003, 2008). However, in the last few years various species of bats have been extending northwards owing to the global climate warming (Kravchenko *et al.*, 2025), and their Fennoscandian populations are becoming more numerous and diverse (Vesterinen *et al.*, 2018; Belkin *et al.*, 2024).

Karelia is the south-eastern part of Fennoscandia. Its prevalent topography is hilly flatland with a transition to upland in the west. Most of Karelia (85%) is covered by forests with both coniferous and deciduous trees. This region also has a wide and highly ramified hydrographic network, with about 73,000 waterbodies and watercourses such as lakes, rivers and wetlands (Litvinenko, 2024). This heterogeneous environment supports a diverse mammalian fauna, including that of bats. Ten bat species occur in Karelia, though the records for summer and winter are different (Belkin *et al.*, 2018, 2021, 2023, 2024). Monitoring of hibernacula has shown that only five chiropterans spend the winter in Karelia: *Eptesicus nilssonii* Keyserling & Blasius, 1839, *Myotis brandtii* (Eversmann, 1845), *M. daubentonii, M. mystacinus* Kuhl, 1817 and *Plecotus auritus* (Linnaeus, 1758). In summer, five more species are present: *M. dasycneme* (Boie, 1825), *M. nattereri* Kuhl, 1817, *Nyctalus noctula* Schreber, 1774, *Vespertilio murinus* (Linnaeus, 1758) and *Pipistrellus nathusii* Keyserling & Blasius, 1839 (Belkin *et al.*, 2023, 2024).

Aquatic habitats are essential for all bats as foraging and drinking grounds as well as ecological corridors for dispersal; for *M. daubentonii* and *M. dasycneme* they are major species-specific habitats (Mysłajek *et al.*, 2007; Siivonen & Wermundsen, 2008; Hagen & Sabo, 2011; Krüger *et al.*, 2012, 2014; Burns *et al.*, 2015; Salvarina, 2016; Ciechanowski, 2015; Bruckner, 2016; Ciechanowski *et al.*, 2017; Todd & Waters, 2017). Karelia, with its extensive hydrographic network, offers abundant favourable habitats for bats, especially in summer.

There have been quite many studies of chiropterans in Karelia, which focused on species composition, abundance, distribution, the use of different waterbodies and the regional features of overwintering (Belkin *et al.*, 2015, 2018, 2019, 2020, 2021, 2023, 2024). They employed car transect surveys with point sampling using a passive ultrasonic detector as well as mist-netting with thorough anatomical examination for precise morphological identification. The latter approach allowed a clear differentiation between *Myotis brandtii* and *M. mystacinus*, which had long been regarded as sibling species because of their close phenotypic similarity and shared habitat preferences (Belkin *et al.*, 2024). Physiological and biochemical adaptations of bats, especially during hibernation, and their ecological responses to life in northern latitudes have also been investigated (Ilyukha *et al.*, 2015; Antonova *et al.*, 2017, 2018, 2022; Kizhina *et al.*, 2018; Uzenbaeva *et al.*, 2019).

At the same time, Karelian bats are understudied in parasitological respect. Parasite data are important both for the health of the bats themselves and for monitoring the health status of other mammals including humans (Dutheil *et al.*, 2021; Twort *et al.*, 2024; Labadie *et al.*, 2025; Ochieng *et al.*, 2025). Parasites can also be used for monitoring the state of the environment and the diet of the hosts (Altringham, 1996; Lewanzik *et al.,* 2019; Kirillova *et al.,* 2022a). Only two publications have specifically addressed their pathogens and parasites in Karelia/Northwestern Russia. One of them has focused on genomic adaptations of Eurasian *Myotis* spp. to fungal diseases (Twort *et al.,* 2024), while the other has provided some parasitological data on *Eptesicus nilssonii*, *Plecotus auritus* and *M. brandtii* in hibernacula (Lebedeva *et al.*, 2020).

In this paper we present new information about the parasitic fauna associated with *M. brandtii* and *M. daubentonii* during the summer period in Karelia, thereby contributing to the inventory of bat parasites in Northwestern Europe. In addition, we provide the first molecular characterization of mites of the genus *Nycteridocoptes* Oudemans, 1898.

Material and methods

The material for the study was collected in Pryazha District, Republic of Karelia, from 29 July to 01 August 2020. By this time the bats born in the year reach the size and weight of adults and become more active (Belkin *et al.*, 2024). Bats were captured in two localities, Lake Kaskesnavolok (61.5994 N, 33.3373 E) and Lakelet Maloe (61.5974 N, 33.3663 E), using nets (two 3 × 6 m mist nets, with 15 mm mesh size). The sampling started at 20:00 h and ended at 03:00 h.

Kaskesnavolok is a mesotrophic lake with the water surface area of 2.5 km^2 and a serrated shoreline 12.6 km long (Filatov & Kukharev, 2013). Lakelet Maloe (120 by 50 m in size) has swampy shores and is situated

300 m from Lake Kaskesnavolok. Both these water bodies are surrounded by secondary mixed coniferous-deciduous forest with numerous old hollowed trees such as pine, spruce, birch and aspen (178 trees/ha). The sampling sites were situated in the immediate vicinity of villages Kaskesnavolok and Kokkoila, with wooden houses and various household and animal-farming buildings. This environment is favourable for chiropterans, nine species of which are present in the area. Recording by the Song Meter SM2 Bat+ ultrasonic detector (USA) showed that the most common species was the Daubenton's bat *Myotis daubentonii* (71.4% and 72.7% at the lake and at the lakelet, respectively) (Belkin *et al.*, 2023).

For the present study, we collected 22 individuals of bats: 18 females of *M. daubentonii* and 4 females of *M. brandtii*. The fact that only female bats were captured suggests that there might be nursery colonies of these species near the sampling site. The captured animals were left in individual containers until 09:00 h, when they were examined, measured with a digital caliper (antebrachium length) and weighed (AND HT-500 electronic scales, Japan). Species identification was based on distinct exterior traits (Kozhurina, 1997). Additionally, cranial features were used to distinguish species of *M. brandtii*/*mystacinus* group (Strelkov & Buntova, 1982). Body weight and antebrachium length of each individual were used to calculate Body Condition Index (BCI) (Vasen'kov & Potapov, 2007). The correlation between BCI and the abundance of parasites was assessed with the help of the correlation analysis (Spearman's (non-parametric) rank-order correlation coefficient).

After being combed for ectoparasites, the bats were mostly used for the physiological study (Iljina *et al.*, 2022). Only the digestive tract was examined for endoparasites, which were collected and processed by standard parasitological methods (Anikanova *et al.*, 2007). Nematodes were cleared in 80% lactic acid and temporarily mounted on glycerol slides. Cestodes were stained with iron acetocarmine, dehydrated through a graded ethanol series, clarified in clove oil and mounted in Canada balsam. Trematodes were stained with acetocarmine, dehydrated, cleared in dimethyl phthalate and mounted in Canada balsam. The ectoparasites were fixed in 70% alcohol and mounted in Faure-Berlese medium for species identification.

Measurements were made with the help of a Levenhuk C1400 NG digital camera attached to Olympus BX-53 microscope using LevenhukToupView image analysis software (ver. 3.5) at the Core Facility of the Karelian Research Centre of the Russian Academy of Sciences, Petrozavodsk, Russia. The identification was performed using the following keys (Shtackelberg, 1970; Tkach & Sharpilo, 1988; Tkach, 1991; Medvedev, 1996; Stanyukovich, 1997; Kudryashova, 1998; Kirillova *et al.*, 2008, 2022b, 2024; Kirillov *et al.*, 2012; Orlova *et al.*, 2015). For ectoparasites, the number of protonymphs (N1), deutonymphs (N2), females (F) and males (M) is given.

Infection indices (prevalence and mean abundance) and their confidence intervals were calculated in Quantitative Parasitology (Reiczigel *et al.*, 2019; Klaschka & Reiczigel, 2021). Following Bush *et al.* (1997), prevalence (P) was considered as the percentage of bat individuals infected (%), while mean abundance (M) was considered as the average number of parasite individuals per host (uninfected hosts were also included in the calculations).

The identification of female mites of the genus *Nycteridocoptes* Oudemans, 1898 was additionally confirmed by molecular methods. Genomic DNA was isolated separately from two ethanol-fixed specimens (an adult and a larva) using DNA-Extran kits (Synthol, Moscow, Russia). The primers for amplification of mitochondrial DNA belonging to cytochrome c oxidase subunit I (*cox1*) were LCO1460 (5'–GGYCAACAAAAATCATAAGATATTGG–3') and HCO2198 (5'–TAAACTCAGGGGGACCAAAAAAATCA–3') (Folmer *et al.*, 1994). The products of PCR were purified using the Cleanup Standard Extraction Kit (Evrogen, Moscow, Russia) following the manufacturer's instructions and then sequenced directly with the automatic sequencing system ABI PRISM 3100-Avant (Applied Biosystems Inc., Foster City, CA, USA). Amplification failed for the larva but was successful for the adult. So, one consensus sequence of 533 bp was assembled in MEGA v.12 (Kumar *et al.*, 2024) and deposited in GenBank with the accession number PV564216. The identity of the newly generated sequence was checked with the Basic Local Alignment Search Tool (BLASTn) (www.ncbi.nih.gov/BLAST/). It was then aligned with those of several members of the order Sarcoptiformes Reuter, 1909 available in GenBank in MEGA v.12.

To assess the phylogenetic relationships of the newly generated sequence for the mite, Bayesian inference analysis was applied to the dataset. Prior to the analysis, the best-fitting GTR + G+ I model was identified with jModelTest v.2.1.2 (Darriba *et al.*, 2012). Bayesian inference analyses were conducted using MrBayes (v.3.2.3) (Ronquist *et al.*, 2012). Markov chain Monte Carlo (MCMC) simulations were run for 1,000,000 generations, log-likelihood scores were plotted, and only the final 75% of trees were used to produce the consensus tree. Posterior probability was calculated to estimate nodal support. FigTree v.1.4 (Rambaut, 2012) was used to visualize the tree.

Results

In total, 16 parasite species were found in the two bat species, *Myotis brandtii* and *M. daubentonii*, examined in our study (Table 1). Endoparasites were represented by eight species (five species of Trematoda, one species of Cestoda and two species of Nematoda). All the helminths were recovered as adults and appeared to be specific parasites of bats. The ectoparasite fauna consisted of eight species, all of them specific to bats. Four species belonged to the class Arachnida

Table 1. List of parasites of *Myotis daubentonii* and *M. brandtii* in Karelia.

Host	*Myotis daubentonii* $n = 18$			*Myotis brandtii* $n = 4$		
Parasite species	P, %	min–max	M	*n*	min–max	M
Trematoda						
Plagiorchis vespertilionis (Müller, 1780)	72 [47–88]	1–85	10.6 [4.1–26.3]	(1)	1	0.25 [0.0–0.5]
P. koreanus (Ogata, 1938)	–	–	–	(1)	2	0.5 [0.0–1]
Prosthodendrium ascidia (Beneden, 1873)	–	–	–	(4)	25–113	59 [27–92]
Parabascus duboisi (Hurkova, 1961) Khotenovsky, 1985	50 [27–73]	2–105	12.9 [5.1–32.4]	(1)	24	6 [0.0–12]
Lecithodendrium linstowi Dollfus, 1931	61 [38–82]	1–463	46 [14.7–149]	–	–	–
Cestoda						
Vampirolepis balsaci (Joyeux et Baer, 1934)	–	–	–	(2)	1–3	1 [0.0–2.2]
Nematoda						
Molinostrongylus spasskii Andrejко, Pintschuk et Skvorzov, 1968	89 [67–98]	4–46	15.4 [10.8–22]	–	–	–
Pterygodermatites bovieri (Blanchard, 1886)	39 [18–62]	17–253	31.5 [10.7–80.1]	–	–	–
ARACHNIDA						
Sarcoptiformes						
Nycteridocoptes poppei Oudemans, 1898	33 [13–59]	1–4	0.6 [0.2–1.2]	–	–	–
Mesostigmata						
Macronyssus diversipilis (Vitzthum, 1920) (130 NI, 12F, 7M)	89 [65–98]	1–18	6.9 [4.2–11.2]	(4)	7–13	9.8 [7.5–11.5]
Spinturnix myoti (Koch, 1836) (78NI, 61NII, 24F, 61M)	100 [81–100]	4–23	12.4 [9.8–15.2]	(4)	1–4	1.7 [1–2.5]
Trombidiformes						
Leptotrombidium sp., larva	6 [0.1–27]	1	0.06 [0–0.17]	–	–	–
INSECTA						
Siphonaptera						
Ischnopsyllus (I.) mysticus Jordan, 1942 (2F, 1M)	–	–	–	(2)	1–2	0.75 [0.0–1.5]
Myodopsylla trisellis Jordan, 1929 (1F)	–	–	–	(1)	1	0.25 [0.0–0.5]
Diptera						
Nycteribia kolenatii Theodor & Moscona, 1954 (18F, 23M)	72 [46–90]	1–8	2.3 [1.3–3.5]	–	–	–
Penicillidia monoceros Speiser, 1900 (1F, 2M)	17 [4–41]	1	0.17 [0–0.3]	–	–	–

Notes: *n* — number of host individuals examined; P — prevalence (%); *n* — number of infected host individuals; min–max — minimum and maximum number of parasites per infected host individual; M — abundance; [95% PI] — confidence interval.

(one species of Sarcoptiformes, two species of Mesostigmata and one species of Trombidiformes), while the other four species belonged to the class Insecta (two species of Siphonaptera and two species of Diptera). Only four parasite species were shared by the two bat hosts: the trematodes *Plagiorchis vespertilionis* (Müller, 1780) and *Parabascus duboisi* (Hurkova, 1961) Khotenovsky, 1985 and the gamasid mites *Macronys-*

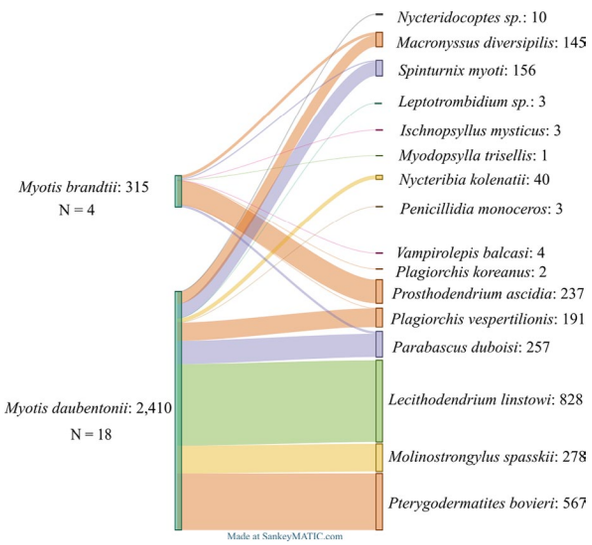


Fig. 1. Host-parasite relationships of *Myotis* spp. and their parasites in Karelia.

sus diversipilis (Vitzthum, 1920) and *Spinturnix myoti* (Koch, 1836) (Fig. 1).

Myotis brandtii hosted nine parasite species (Table 1), with helminths represented by trematodes and cestodes. The trematode *Prosthodendrium ascidia* (Beneden, 1873) was the most abundant species (mean intensity was 59 ind.). Another trematode, *P. duboisi*, was represented by 24 worms obtained from a single individual of *M. brandtii*. Other helminth species were represented by one worm each. Ectoparasites collected from *M. brandtii* were represented by only four species: two species of gamasid mites, *Macronyssus diversipilis* (only protonymphs, 28 ind.) and *Spinturnix myoti* (1N1, 3F, 2M), and two species of fleas from the family Ischnopsyllidae Wahlgren, 1907 (Table 1).

The parasitic assemblage of *Myotis daubentonii* was more diverse and comprised 11 species (Table 1, Fig. 1). Helminths were represented by five species (three trematodes and two nematodes), the most abundant being *Lecithodendrium linstowi* Dollfus, 1931 (P 61%; M 46) and *Pterygodermatites bovieri* (Blanchard, 1886) (P 39%; M 31.5).

Ectoparasites of *M. daubentonii* were represented by six species (Table 1). All individuals of *M. daubentonii* examined in our study were infested with *S. myoti*, with intensities ranging from 4 to 24 mites per host (totalling 77N1, 61N2, 21F and 59M). The prevalence and mean abundance of *M. diversipilis* on *M. daubentonii* were 89% and 6.9, respectively, with a total sample size of 102 protonymphs, 12 females and 7 males (Table 1).

Adult females of *Nycteridocoptes* sp. (Sarcoptiformes) enclosed in small, more or less transparent keratinous sacs were found on the patagium of six out of 18 examined individuals of *M. daubentonii* (Table 1). Each sac contained one large gravid female as well as laid eggs and hatched larvae. Considering the morphology and the host specificity, we assumed that

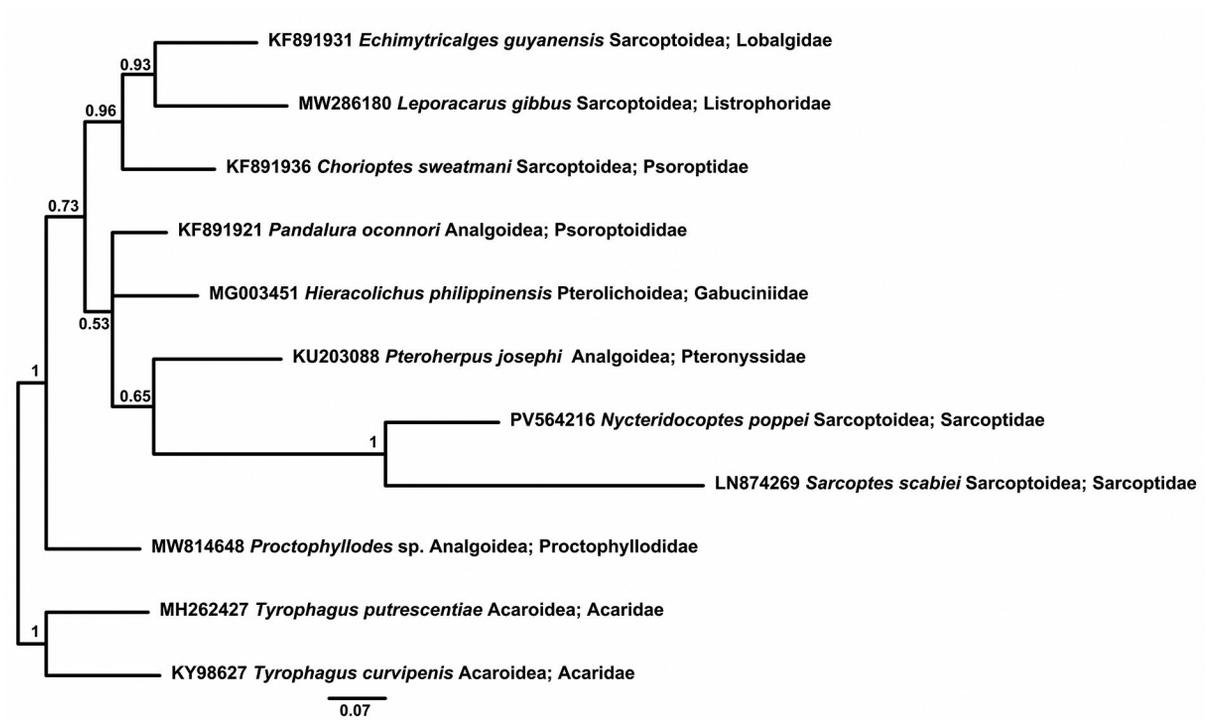


Fig. 2. Phylogenetic position of *Nycteridocoptes poppei* Oudemans, 1898 in the order Sarcoptiformes according to Bayesian Inference with GTR+G + I model.

these mites belonged to *Nycteridocoptes poppei* Oudemans, 1898, a species known from European *Myotis* bats (Fain & Aellen, 1961; Klompen, 1992; Bochkov, 2010). Additionally, we characterised these mites using molecular analysis. A partial cytochrome c oxidase subunit 1 (*cox1*) sequence (533 bp) was obtained for mites *Nycteridocoptes poppei* for the first time. Phylogenetic analysis showed that the species is most closely related to *Sarcoptes scabiei* (Linnaeus, 1758), one of the members of the family Sarcoptidae represented in Genbank (Fig. 2).

Two species of nycteribiid flies (Insecta, Diptera) were found on *M. daubentonii*: *Nycteribia kolenatii* Theodor & Moscona, 1954 (18F and 23M) and *Penicillidia monoceros* Speiser, 1900 (1F and 2M) (Table 1).

Mean weights and antebrachium length of the female bats were 8.2 g (6.3–9.8), 38.4 mm (36.7–40.1) and 6.2 g (5.9–6.6), 35.3 mm (34.9–35.7) for *M. daubentonii* and *M. brandtii*, respectively. Body condition index (BCI), which was calculated for each bat examined in our study, made up, on average, 1.05 for *M. daubentonii* and 1.21 for *M. brandtii*. While larger individuals of *M. daubentonii* were infected by a greater number of parasites (Fig. 3), we did not find any correlation between BCI and the abundance of any parasite species or group (trematodes, nematodes, gamasid mites) ($p > 0.05$).

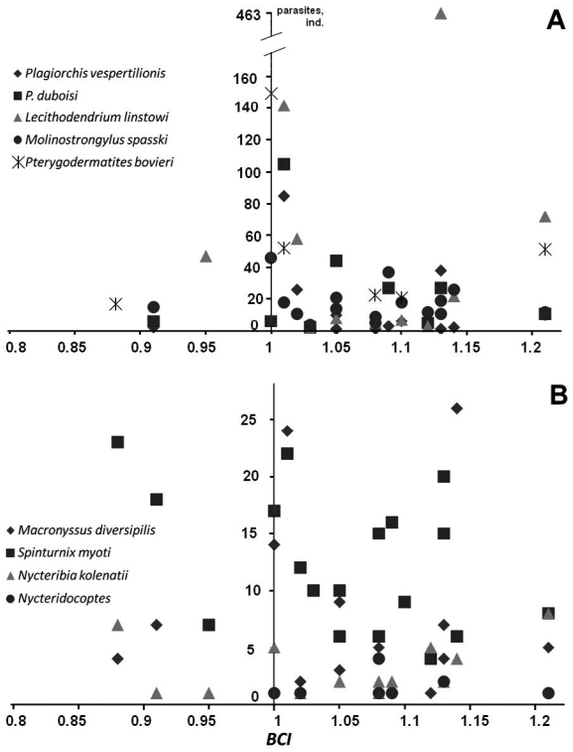


Fig. 3. Number of parasites in individuals of *Myotis daubentonii* differing in the body condition index (BCI): A — helminths; B — ectoparasites.

Discussion

Our parasitological survey showed that *Myotis brandtii* and *M. daubentonii* hosted 16 parasite species (8 helminths and 8 ectoparasites). Eleven of them were found in Karelia for the first time: the trematodes *Prosthodendrium ascidia* and *Parabascus duboisi*, the cestode *Vampirolepis balsaci*, the nematodes *Molinostrongylus spasskii* and *Pterygodermatites bovieri*,

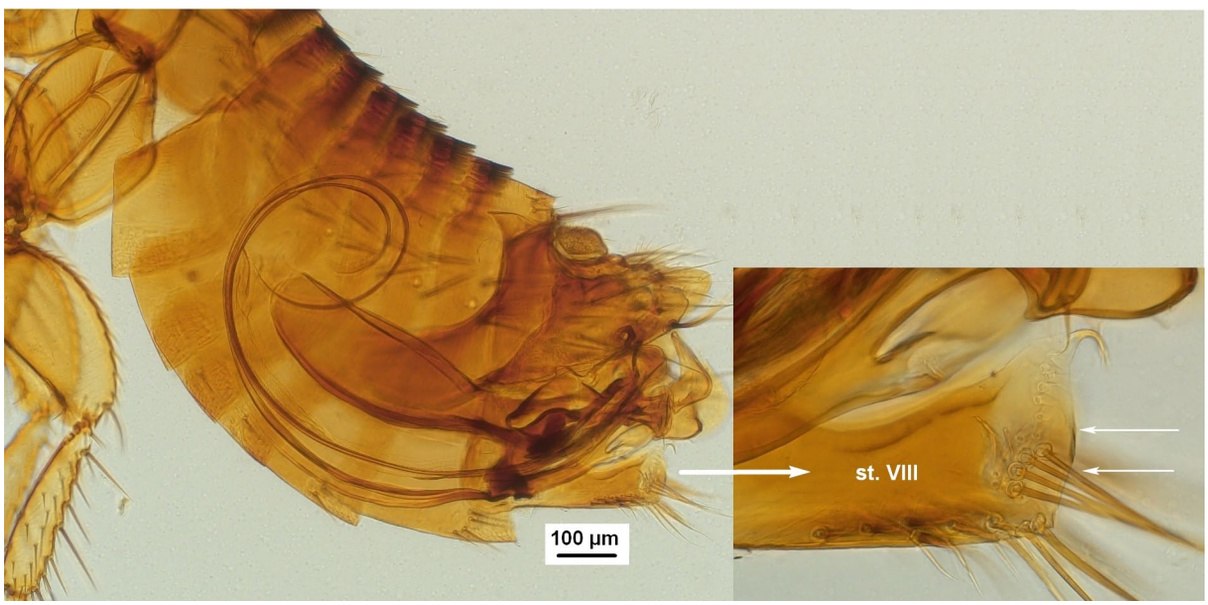


Fig. 4. *Ischnopsyllus* (*I.*) *s. mysticus*, Male — apical margin of sternum VIII not incurved below the apical hook and none of the apical setae flattened.

two species of Mesostigmata, two species of Diptera as well as fleas *Ischnopsyllus (I.) mysticus* and *Myodopsylla trisellis.*The parasite fauna of *M. brandtii* was less diverse, with both species richness and infection rates being lower than in *M. daubentonii* (Table 1, Fig. 1). While these differences may be partly associated with the smaller sample size of *M. brandtii* in our study ($n = 4$), they are probably mostly due to the ecological niche differentiation of these two bats expressed in different characteristics of the nursery colonies, spatial distribution, foraging habitats and diet.

Most helminth infections are acquired trophically, which is associated with the complex life cycles of these parasites. Trematodes recorded in our study use various insects as second intermediate hosts. For *Plagiorchis* spp., these are different taxa from the orders Diptera, Trichoptera, Ephemeroptera, Chironomidae, Megaloptera and Odonata (Ilyushina, 1975; Sudarikov *et al*., 2002). While the life cycles of *Prosthodendrium ascidia* and *Lecithodendrium linstowi* are characterized incompletely, these trematodes probably use aquatic insect larvae from the orders Trichoptera, Ephemeroptera, Megaloptera and Odonata, as do other members of the families Pleurogenidae and Lecithodendriidae (Ilyushina, 1975; Sudarikov *et al.*, 2002). Infection of bats with cestodes *Vampirolepis* spp. was probably the result of accidental ingestion of infected fleas *Ischnopsyllus* spp. (Frank *et al.*, 2015). The nematode *Pterygodermatites bovieri* uses insect intermediate hosts, whereas *Molinostrongylus spasskii* has a direct life cycle (Kirillova *et al.*, 2008).

The helminth assemblages of *M. brandtii* and *M. daubentonii* reflect their dietary habits. Out of the eight helminth species recorded in our study, these two bats share only two, *Parabascus duboisi* and *Plagiorchis vespertilionis*, which indicates that the overlap in their diet is minimal. The infection rates of these trematodes are substantially lower in *M. brandtii* than in *M. daubentonii* (Table 1, Fig. 1), which is probably associated with the differences in prey composition. *Myotis brandtii* primarily captures small insects (in flight in open or semi-open habitats), mainly lepidopterans, especially moths from the families Tortricidae and Geometridae, but also mosquitoes, midges and flies (Vesterinen *et al.*, 2018). In central Russia, its diet also includes mosquitoes from the families Chironomidae and Culicidae as well as coleopterans (Smirnov & Vekhnik, 2012, 2014). In contrast, *M. daubentonii* mostly preys on dipterans, with a substantial addition of trichopterans and coleopterans (Vesterinen *et al.*, 2016, 2018). In particular, this trawling species readily consumes chironomid midges from water surfaces. This explains its diverse helminth fauna, including three trematode species whose intermediate hosts are aquatic insects and the nematode *Pterygodermatites bovieri*, which uses beetles as intermediate hosts. Only *M. brandtii* was infected with the cestode *Vampirolepis balsaci*, which was probably acquired through accidental ingestion of *Ischnopsyllus* fleas found on this host (see above).

Well-documented seasonal variations in parasitic communities of bats are largely driven by the synchrony between the life cycles of the host and the parasite (Markova, 1938; Krasnolobova, 1979; Zahn & Rupp, 2004; Chikhlyaev *et al.*, 2012; Kirillov *et al.*, 2012). Previous studies of parasitic fauna of bats in Karelia were conducted only during the winter hibernation (Lebedeva *et al.*, 2020). In the present study the samples were collected in late July, which is the breeding season of bats and the peak of their foraging activity. As a result, we expanded the list of parasites recorded in these hosts. Notably, a single *M. brandtii* individual collected from a cave hibernaculum hosted only four trematodes (*Plagiorchis vespertilionis, P. koreanus, P. muelleri*, and *Lecithodendrium linstowi*), with the former and the latter species being the most abundant. In summer, *M. brandtii* had a richer parasitic fauna, but infection with *P. vespertilionis* was low and that with *L. linstowi* was absent. These differences probably reflect seasonal variations in the availability of intermediate hosts as well as dietary shifts.

The species composition of ectoparasites and their infection rates also differed in the two *Myotis* spp. The ectoparasite fauna of *M. daubentonii* was more diverse and included two species of Nycteribiidae, one species of Sarcoptiformes and one species Trombidiformes, none of which were found on *M. brandtii*. At the same time, fleas were found only on *M. brandtii*, despite the small sample. Infection rates of *Macronyssus diversipilis* were comparable in *M. brandtii* and *M. daubentonii*, while the infestation intensity of *Spinturnix myoti* was higher in *M. daubentonii* (Table 1). The only ectoparasites shared by *M. brandtii* and *M. daubentonii* were two mites from the order Mesostigmata.

Our finding of the mite *Nycteridocoptes poppei* Oudemans, 1898 on *M. daubentonii* is the northernmost detection of this species in Europe. Further south, it has been found on various *Myotis* spp., including *M. daubentonii*, in Germany, France, Belgium and Great Britain (Fain & Aellen, 1961; Baker & Craven, 2003; Rupp *et al.*, 2004; Frank *et al.*, 2015; Léger, 2020). Its absence in earlier studies in northern Palearctic may reflect its low abundance and short adult lifespan. In our survey, *N. poppei* was recorded in bats from both of the two study localities possibly representing different nursery colonies.

The finding of the flea *Ischnopsyllus* (*I.*) *mysticus* in mid-boreal Karelia is noteworthy. One of the two individuals found in our study was a male (Fig. 4), which definitively confirms the presence of this species (or subspecies) in Northwestern Russia (females of *Ischnopsyllus simplex* and *I. mysticus* are morphologically indistinguishable). In previous surveys of *M. brandtii* in hibernacula in Karelia, we found only female *Ischnopsyllus simplex/mysticus* specimens (Lebedeva *et al.*, 2020). In Northwestern Europe, *I. mysticus* has been recorded from *Myotis* spp. in Denmark, Norway and Finland (Brinck-Lindroth & Smit, 2007). In Estonia, it is known only from *M. brandtii* (Medvedev & Mazing, 1987). The confirmed finding of *Ischnopsyllus* (*I.*) *mysticus* in Karelia is the first registration of this species in Russia. It is not mentioned in the faunistic review of fleas from bats

in the Russian Federation (Orlova *et al.*, 2025), which contains data on 18 species from 44 locations.

We could not conduct the ecological factor analysis of prevalence of different parasite groups in *M. brandtii* and *M. daubentonii* because of the small number of bat individuals examined in our study. Nevetheless, the species composition of the parasites found in our study may in itself be an important ecological characteristic of bats in the north part of their range. Overall, the parasite assemblages of both *M. brandtii* and *M. daubentonii* in Karelia consisted predominantly of widespread parasites associated with bats, whose distributions overlap those of their hosts (Stanjukovich, 1990; Shimalov *et al.*, 2002; Virta, 2014; Frank *et al.*, 2015; Siepel *et al.*, 2016; Kirillov *et al.*, 2018; Sümer & Yıldırımhan, 2019; Léger, 2020; Kirillova *et al.*, 2022a, 2023; Budinski & López-Baucells, 2023; Encarnação & Becker, 2023; Evsyukov & Tsygankova, 2023, 2024; Evsyukov & Potapenko, 2024; Evsyukov *et al*., 2024). For a more comprehensive understanding of the host-parasite interactions, further investigations are required, including detailed studies of insect prey diversity and their role in helminth life cycles.

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References

Altringham J.D. 1996. Bats: Biology and Behaviour. Oxford: Oxfrod University Press. 262 p.

Anikanova V.S., Bugmyrin S.V. & Ieshko E.P. 2007. [Methods of the Collection and Studies of Helminths of Small Mammals]. Petrozavodsk: Karelian Scientific Center of RAS. 145 p. [In Russian]

Antonova E.P., Ilyukha V.A., Sergina S.N., Khizhkin E.A., Belkin V.V., Yakimova A.E. & Morozov A.A. 2017. Antioxidant defenses in three vesper bats (Chiroptera: Vespertilionidae) during hibernation // Turkish Journal of Zoology**.** Vol.41. P.1005–1009. DOI: 10.3906/zoo-1702-53

Antonova E.P., Ilyukha V.A., Sergina S.N., Unzhakov A.R. & Belkin V.V. 2018. Lactate dehydrogenase isozymes in the tissues of hibernating bats (Chiroptera) // Biophysics. Vol.63. P.116–121. DOI: 10.1134/S0006350918010037

Antonova E.P., Belkin V.V., Ilyukha V.A., Khizhkin E.A. & Kalinina S.N. 2022. Seasonal changes in body mass and activity of digestive enzymes in *Eptesicus nilssonii* (Mammalia: Chiroptera: Vespertilionidae) during Hibernation // Journal of Evolutionary Biochemistry and Physiology. Vol.58. P.1055–1064. DOI: 10.1134/S002209302204010X

Baker A.S. & Craven J.C. 2003. Checklist of the mites (Arachnida: Acari) associated with bats (Mammalia: Chiroptera) in the British Isles // Systematic and Applied Acarology. Vol.14. P.1–20. DOI: 10.11158/saasp.14.1.1

Belkin V.V., Panchenko D.V., Tirronen K.F., Yakimova A.E. & Fedorov F.V. 2015. Ecological status of bats (Chiroptera) in winter roosts in eastern Fennoscandia // Russian Journal of Ecology. Vol.46. P.463–469. DOI: 10.1134/S1067413615050045

Belkin V., Ilyukha V., Khizhkin E., Fyodorov F., Morozov A. & Yakimova A. 2018. [Species diversity and distribution of Chiroptera (Vespertilionidae) in Karelia] // Principy Ekologii. Vol.3. P.13–23 [in Russian]. DOI: 10.15393/j1.art.2018.8042

Belkin V.V., Ilyukha V.A., Khizhkin E.A., Fyodorov F.V. & Yakimova A.E. 2019. [Studies of the bat fauna (Mammalia, Chiroptera) in the Green Belt of Fennoscandia] // Transactions of KarRC RAS. No.5. P.17–29 [in Russian]. DOI: 10.17076/eco1079

Belkin V.V., Ilyukha V.A., Khizhkin E.A., Yakimova A.E., Fyodorov F.V., Antonova E.P., Kizhina A.G., Uzenbaeva L.B., Ilyina T.N. & Baishnikova I.V. 2020. [Ecological and physiological- biochemical adaptation of the northern bat (*Eptesicus nilssonii* L.) as a factor of the species dominance in northern latitudes] // Transactions of Kola Science Centre. No.11. P.69–83 [in Russian]. DOI: 10.37614/2307-5252.2020.2.8.007

Belkin V.V., Fyodorov F.V., Ilyukha V.A. & Yakimova A.E. 2021. Characteristics of the bat (Chiroptera) population in protected areas in the northern and middle taiga subzones of European Russia // Nature Conservation Research. Vol.6. P.17–31. DOI: 10.24189/ncr.2021.002

Belkin V.V., Ilyukha V.A., Khizhkin E.A., Lyapunov A.N. & Tolstoguzov A.O. 2023. Chiropterans (Chiroptera) in Lake–River Systems of Northern European Russia // Biology Bulletin. Vol.50. P.2034–2044. DOI: 10.1134/s1062359023080058

Belkin V.V., Ilyukha V.A., Chistyakov D.V., Fyodorov F.V., Lyapunov A.N. & Khizhkin E.A. 2024. Summer chiropteran community in the Sergievka Park with the unique dominance of *Pipistrellus nathusii* on the northern periphery of its distribution range // Baltic Forestry. Vol.30. No.1. Art.756. DOI: 10.46490/BF756

Bochkov A.V. 2010. A review of mammal-associated Psoroptidia (Acariformes: Astigmata) // Acarina. Vol.18. P.99–260.

Brinck-Lindroth G. & Smit F.G.A.M. 2007. The Fleas (Siphonaptera) of Fennoscandia and Denmark. Leiden, Boston: Brill. 185 p.

Bruckner A. 2016. Recording at water bodies increases the efficiency of a survey of temperate bats with stationary, automated detectors // Mammalia. Vol.80. P.645–653. DOI: 10.1515/mammalia-2014-0067

Budinski I. & López-Baucells A. 2023. *Myotis mystacinus* species complex (*M. mystacinus*, *M. brandtii*, *M. alcathoe*, *M. davidii*) // Russo D. (ed.). Handbook of the Mammals of Europe. Chiroptera. Cham: Springer Nature. P.321–353. DOI: 10.1007/978-3-319-65038-8_53-1

Burns L.E., Segers J.L. & Broders H.G. 2015. Bat activity and community composition in the northern boreal forest of south-central Labrador, Canada // Northeastern Naturalist. Vol.22. P.32–40. DOI: 10.1656/045.022.0109

Bush A.O., Lafferty K.D., Lotz J.M. & Shostak A.W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited // Journal of Parasitology. Vol.83. P.575–583. DOI: 10.2307/3284227

Ciechanowski M. 2015. Habitat preferences of bats in anthropogenically altered, mosaic landscapes of northern

Poland // European Journal of Wildlife Research. Vol.61. P.415–428. DOI: 10.1007/s10344-015-0911-y

Ciechanowski M., Zapart A., Kokurewicz T., Rusiński M. & Lazarus M. 2017. Habitat selection of the pond bat (*Myotis dasycneme*) during pregnancy and lactation in northern Poland // Journal of Mammalogy. Vol.98. P.232–245. DOI: 10.1093/jmammal/gyw108

Chikhlyaev I.V., Kirillova N.Y. & Kirillov A.A. 2012. [Characteristic of life cycles of trematodes (Trematoda) of land vertebrates from the Middle Volga Region] // Izvestia of Samara Scientific Center of the Russian Academy of Sciences. Vol.14. P.132–142 [in Russian].

Darriba D., Taboada G.L., Doallo R. & Posada D. 2012. jModelTest 2: More models, new heuristics and parallel computing // Nature Methods. Vol.9. Art.772. DOI: 10.1038/nmeth.2109

Dutheil F., Clinchamps M. & Bouillon-Minois J.B. 2021. Bats, pathogens, and species richness // Pathogens. Vol.21. Art.98. DOI: 10.3390/pathogens10020098

Encarnação J.A. & Becker N.I. 2023. Daubenton's bat *Myotis daubentonii* (Kuhl, 1817) // Russo D. (ed.). Handbook of the Mammals of Europe. Chiroptera. Cham: Springer Nature. P.225–256. DOI: 10.1007/978-3-319-65038-8_49-1

Evsyukov A.P. & Tsygankova M.G. 2023. [Helminth fauna of bats in the Rostov Region: review. 1. Nematoda] // Russian Journal of Veterinary Pathology. Vol.22. P.5–16 [in Russian]. DOI: 10.23947/2949-4826-2023-22-3-5-16

Evsyukov A.P. & Tsygankova M.G. 2024. [Helminth fauna of bats of the Rostov Region: review. 2. Trematoda] // Russian Journal of Veterinary Pathology. Vol.23. P.7–20 [in Russian]. DOI: 10.23947/2949-4826-2024-23-1-7-20

Evsyukov A.P. & Potapenko I.O. 2024. [Helminth fauna of bats of the Rostov Region: review. 4. Acanthocephala. General conclusions] // Russian Journal of Veterinary Pathology. Vol.23. P.7–14 [in Russian]. DOI: 10.23947/2949-4826-2024-23-4-7-14

Evsyukov A.P., Potapenko I.O. & Tsygankova M.G. 2024. [Helminth fauna of bats of the Rostov Region: review. 3. Cestoda] // Russian Journal of Veterinary Pathology. Vol.23. P.7–14 [in Russian]. DOI: 10.23947/2949-4826-2024-23-2-7-14

Fain A. & Aellen V. 1961. Les acariens psoriques parasites des chauves-souris. XX. Un cas d'hyperparasitisme par *Nycteridocoptes poppei*. Nouvelles observations sur l'évolution cyclique de la gale sarcoptique chez les chiroptères // Revue Suisse de Zoologie. Vol.68. P.305–309. DOI: 10.5962/bhl.part.75087

Filatov N.N. & Kukharev V.I. 2013. [Lakes of Karelia. Reference Book]. Petrozavodsk: KarRC RAS. 464 p. [In Russian]

Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates // Molecular Marine Biology and Biotechnology. Vol.3. P.294–299.

Frank R., Kuhn T., Werblow A., Liston A., Kochmann J. & Klimpel S. 2015. Parasite diversity of European *Myotis* species with special emphasis on *Myotis myotis* (Microchiroptera, Vespertilionidae) from a typical nursery roost // Parasites & Vectors. Vol.8. Art.101. DOI: 10.1186/s13071-015-0707-7

Hagen E. & Sabo J. 2011. A landscape perspective on bat foraging ecology along rivers: does channel confinement and insect availability influence the response of bats to aquatic resources in riverine landscapes? // Oecologia. Vol.166. P.751–760. DOI: 10.1007/s00442-011-1913-4

Iljina T.N., Baishnikova I.V. & Belkin V.V. 2022. Retinol and α-tocopherol content in the liver and skeletal muscle of bats (Chiroptera) during hibernation and summer activity // Journal of Evolutionary Biochemistry and Physiology. Vol.58. P.1697–1707. DOI: 10.1134/S0022093022060035

Ilyukha V.A., Antonova E.P., Belkin V.V., Uzenbaeva L.B., Khizhkin E.A., Sergina S.S., Ilyina T.N., Baishnikova I.V., Kizhina A.G. & Yakimova A.E. 2015. The eco-physiological status of hibernating bats (Chiroptera) in the north of the European distribution range // Acta Biologica Universitatis Daugavpiliensis. Vol.15. P.75–94.

Ilyushina T.Y. 1975. [The role of aquatic insects in the life cycle of trematodes] // Ryzhikov K.M. & Folitarek S.S. (eds.). [Parasites in the Natural Complexes of Northern Kulunda]. Novosibirsk: Nauka. P.53–94 [in Russian].

Kirillov A.A., Kirillova N.Y. & Chikhlyaev I.V. 2018. [Parasites of Vertebrate Animals of the Samara Region]. Togliatti: Poliar. 304 p. [In Russian]

Kirillov A.A., Kirillova N.Y. & Vekhnik V.P. 2012. [Trematodes (Trematoda) of bats (Chiroptera) from the Middle Volga] // Parazitologiya. Vol.46. P.384–413 [in Russian].

Kirillova N.Y., Kirillov A.A., Shchenkov S.V., Knyazev A.E. & Vekhnik V.A. 2024. Morphological and molecular characterization of plagiorchiid trematodes (*Plagiorchis*: Plagiorchiidae, Digenea) from bats with redescription of *Plagiorchis mordovii* Shaldybin, 1958 // Journal of Helminthology. Vol.98. Art.e2. DOI: 10.1017/S0022149X23000913

Kirillova N.Y., Kirillov A.A. & Vekhnik V.A. 2008. [Nematodes (Nematoda) of bats (Chiroptera) of Samarskaya Luka (Russia)] // Parazitologiya. Vol.42. P.526–532 [in Russian].

Kirillova N.Y., Kirillov, A.A. & Vekhnik V.A. 2022a. [Comparative analysis of helminth fauna of *Myotis brandtii* and *Myotis mystacinus* (Chirterga, Vespertilionidae) of Samarskaya Luka National Park (Russia)] // Nature Conservation Research. Vol.7. P.1–14 [in Russian]. DOI: 10.24189/ncr.2022.026

Kirillova N.Y., Kirillov A.A. & Vekhnik V.A. 2023. The diversity of trematodes in *Myotis* bats (Chiroptera, Vespertilionidae) from the Samarskaya Luka (European Russia) // Animals. Vol.13. Art.3738. DOI: 10.3390/ani13233738

Kirillova N.Y., Shchenkov S.V., Kirillov A.A. & Ruchin A.B. 2022b. Trematodes of genera *Gyrabascus* and *Parabascus* from bats in European Russia: morphology and molecular phylogeny // Biology. Vol.11. Art.878. DOI: 10.3390/biology11060878

Kizhina A., Uzenbaeva L., Antonova E., Belkin V., Ilyukha V. & Khizhkin E. 2018. Hematological parameters in hibernating *Eptesicus nilssonii* (Mammalia: Chiroptera) collected in Northern European Russia // Acta Chiropterologica. Vol.20. P.273–283. DOI: 10.3161/15081109ACC2018.20.1.021

Klaschka J. & Reiczigel J. 2021. On matching confidence intervals and tests for some discrete distributions: methodological and computational aspects // Computational Statistics. Vol.36. P.1775–1790. DOI: 10.1007/s00180-020-00986-0

Klompen J.S.H. 1992. Phylogenetic relationships in the mite family Sarcoptidae (Acari: Astigmata) // Miscellaneous Publications of the Museum of Zoology. No.180. Michigan: University of Michigan. P.1–154.

Kozhurina E.I. 1997. [Bats of the European part of the former USSR. Field identifier by external features]. [Electronic resource]. http://www.chiroptera.ru/content-view-1.html [in Russian].

Krasnolobova T.A. 1979. [Study of biological peculiarities of *Plagiorchis elegans* in the Volga delta] // Trudy Gelminthologicheskoy Laboratorii of the USSR Academy of Sciences. Vol.29. P.75–80 [in Russian].

Kravchenko K., Voig C.C., Volkholz J., Courtiol A. & Currie S.E. 2025. Shorter and warmer winters expand the hibernation area of bats in Europe // Ecology Letters. Vol.28. Art.e70119. DOI: 10.1111/ele.70119

Krüger F., Harms I., Fichtner A., Wolz I. & Sommer R. 2012. High trophic similarity in the sympatric North European trawling bat species *Myotis daubentonii* and *Myotis dasycneme* // Acta Chiropterologica. Vol.14. P.347–356.

Krüger F., Clare E.L., Greif S., Siemers B.M., Symondson W.O. & Sommer R.S. 2014. An integrative approach to detect subtle trophic niche differentiation in the sympatric trawling bat species *Myotis dasycneme* and *Myotis daubentonii* // Molecular Ecology. Vol.23. P.3657–3671. DOI: 10.1111/mec.12512

Kudryashova N.I. 1998. [Chigger Mites (Acariformes, Trombiculidae) of the Eastern Palaearctic]. Moscow: KMK Scientific Press. 342 p. [In Russian]

Kumar S., Stecher G., Suleski M., Sanderford M., Sharma S. & Tamura K. 2024. MEGA12: Molecular Evolutionary Genetics Analysis version 12 for adaptive and green computing // Molecular Biology and Evolution. Vol.41. P.1–9. DOI: 10.1093/molbev/msae263

Labadie M., Morand S., Bourgarel M., Niama F.R., Nguilili G.F., Tobi N., Caron A. & De Nys H. 2025. Habitat sharing and interspecies interactions in caves used by bats in the Republic of Congo // PeerJ. Vol.9. Art.e18145. DOI: 10.7717/peerj.18145

Lebedeva D.I., Belkin V.V., Stanyukovich M.K., Bespyatova L.A. & Bugmyrin S.V. 2020. First records of bat parasites in Karelia // Transactions of KarRC RAS. No.8. P.120–125. DOI: 10.17076/bg1142

Léger C. 2020. Bat parasites (Acari, Anoplura, Cestoda, Diptera, Hemiptera, Nematoda, Siphonaptera, Trematoda) in France (1762–2018): a literature review and contribution to a checklist // Parasite. Vol.27. Art.61. DOI: 10.1051/parasite/2020051

Lewanzik D., Sundaramurthy A.K. & Goerlitz H.R. 2019. Insectivorous bats integrate social information about species identity, conspecific activity and prey abundance to estimate cost–benefit ratio of interactions // Journal of Animal Ecology. Vol.88. P.1462–1473. DOI: 10.1111/1365-2656.12989

Litvinenko A.V. 2024. [A comprehensive account of the Karelian water network] // Transactions of KarRC RAS. No.2. P.6–24 [in Russian]. DOI: 10.17076/lim1829

Markova L.I. 1938. [Influence of winter hibernation on the state of parasitofauna of bats] // Zoologicheskii zhurnal. Vol.17. P.133–145 [in Russian].

Medvedev S.G. 1996. Fleas of the family Ischnopsyllidae (Siphonaptera) of the fauna of Russia and adjacent countries // Entomological Review. Vol.76. P.480–493.

Medvedev S.G. & Mazing M.V. 1987. [Fleas of the family Ischnopsyllidae (Siphonaptera) from the Baltic Region] // Parazitologiya. Vol.21. P.459–466 [in Russian].

Mysłajek R.W., Kurek K., Szura C., Nowak S. & Orysiak P. 2007. Bats (Chiroptera) of the Silesian Beskid Mountains // Fragmenta Faunistica. Vol.50. P.77–85.

Ochieng J.R., Kato C.D. & Kisakye J.J.M. 2025. Gastrointestinal parasites of zoonotic importance detected in bats in the conservation area of Semuliki National Park, western Uganda // Journal of Parasitology Research. Art.9972163. DOI: 10.1155/japr/9972163

Orlova M.V., Stanyukovich M.K. & Orlov O.L. 2015. Gamasid Mites (Mesostigmata: Gamasina) Associated with Bats (Chiroptera: Vespertilionidae, Rhinolophidae, Molossidae) of Boreal Palaearctic Zone (Russia and adjacent countries). Tomsk: Publishing House of Tomsk State University. 150 p.

Orlova M.V., Viskontene A.L., Korzikov V.A., Zabashta M.V., Zabashta A.V., Kruskop S.V., Smirnov D.G., Malyavina M.S., Pavlov A.V., Orlov O.L., Mishchenko V. A., Vyalykh I. V., Boyarintsev D.I., Kuzminov I.V., Bryutova K., Khizhkin E.A., Larchanka A.I., Shapkin O.A., Vinogradova E.A. & Sakharov S.P. 2025. A review of bat fleas (Siphonaptera: Ischnopsyllidae) from Russia // Diversity. Vol.17. Art.419. DOI: 10.3390/d17060419

Rambaut A. 2012. FigTree v1. 4. Molecular evolution, phylogenetics and epidemiology. https://github.com/rambaut/figtree/releases.

Reiczigel J., Marozzi M., Fabian I. & Rozsa L. 2019. Biostatistics for parasitologists — a primer to quantitative parasitology // Trends in Parasitology. Vol.35. P.277–281. DOI: 10.1016/j.pt.2019.01.003

Ronquist F., Teslenko M., Van Der Mark P., Ayres D.L., Darling A., Höhna S. & Huelsenbeck J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space // Systematic Biology. Vol.61. P.539–542. DOI: 10.1093/sysbio/sys029

Rupp D., Zahn A. & Ludwig P. 2004. Actual records of bat ectoparasites in Bavaria (Germany) // Spixiana. Vol.27. P.185–190.

Salvarina I. 2016. Bats and aquatic habitats: a review of habitat use and anthropogenic impacts // Mammal Review. Vol.46. P.131–143. DOI: 10.1111/mam.12059

Shimalov V., Demyanchik M. & Demyanchik V. 2002. A study on the helminth fauna of the bats (Mammalia, Chiroptera: Vespertilionidae) in Belarus // Parasitology Research. Vol.88. P.1011. DOI: 10.1007/s004360100415

Shtackelberg A.A. 1970. [Family Nycteribiidae] // Bey-Bienko G.Y. (ed.). [Key to Insects of the European Part of the USSR]. Leningrad: Nauka. P.603–607 [in Russian].

Siepel H., Cremers H. & Vierbergen B. 2016. Provisional checklist of the astigmatic mites of the Netherlands (Acari: Oribatida: Astigmatina) // Nederlandse Faunistische Mededelingen. Vol.47. P.49–87.

Siivonen Y. & Sulkava S. 1999. Mammals of the North. Helsinki: Otava. 224 p.

Siivonen Y. & Wermundsen T. 2003. First records of *Myotis dasycneme* and *Pipistrellus pipistrellus* in Finland // Vespertilio. Vol.7. P.177–179.

Siivonen Y. & Wermundsen T. 2008. Distribution and foraging habitats of bats in northern Finland: *Myotis daubentonii* occurs north of the Arctic Circle // Vespertilio. Vol.12. P.41–48.

Simmons N.B. 2005. Order Chiroptera // Wilson D.E. & Reeder D.M. (eds.). Mammal Species of the World: A Taxonomic and Geographic Reference. Third edition. Baltimore: Johns Hopkins University Press. P.312–529.

Smirnov D.G. & Vehnik V.P. 2012. [Biotopic structure of the communities of mammals of floodplain ecosystems of Samarskaya Luka] // Izvestia of Samara Scientific Center of the Russian Academy of Sciences. Vol.14. P.177–180 [in Russian].

Smirnov D.G. & Vehnik V.P. 2014. Ecology of nutrition and differentiation of the trophic niches of bats (Chiroptera: Vespertilionidae) in floodplain ecosystems of the Samara Bend // Biology Bulletin. Vol.41. P.60–70. DOI: 10.1134/S1062359014010105

Stanjukovich M.K. 1990. [The gamasid mites and argasid ticks of bats from the Baltic area and Leningrad Region] // Parazitologiya. Vol.24. P.193–200 [in Russian].

Stanyukovich M.K. 1997. Keys to gamasid mites (Acari, Parasitiformes, Mesostigmata, Macronyssoidea et Laelaptoidae) parasitizing bats (Mammalia, Chiroptera) from Russia and adjacent countries // Rudolstadter Naturhistorische Schriften. Vol.7. P.13–46.

Strelkov P.P. & Buntova E.G. 1982. [The whiskered bat (*Myotis mystacinus*) and the Brandt's bat (*Myotis brandti*) in the USSR and interrelations of these species. Report. 1] // Zoologicheskii Zhurnal. Vol.61. P.1227–1241 [in Russian].

Sudarikov V.E., Shigin A.A., Kurochkin Yu.V., Stenko R.P. & Yurlova N.I. 2002. [Metacercariae of Trematodes — Parasites of Hydrobionts of Russia]. Moscow: Nauka. 296 p. [In Russian]

Sümer N. & Yildirimhan H.S. 2017. DNA sequencing of Digenea nuclear lsrDNA of the whiskered brown bat, *Myotis aurescens* (Vespertilionidae: Chiroptera), from Turkey // Turkish Journal of Zoology. Vol.41. P.64–66. DOI: 10.3906/zoo-1508-52

Tkach V.V. 1991. [First finding of males of *Pterigotrematites bovieri* (Nematoda, Rectulariidae) parazitizing bats] // Zoologicheskii Zhurnal. Vol.70. P.125–127 [in Russian].

Tkach V. & Sharpilo L.D. 1988. [Nematodes of the genus *Molinostrongylus* (Nematoda, Molineidae) from Ukrainian bats] // Vestnik Zoologii. Vol.4. P.3–8 [in Russian].

Todd V.L.G. & Waters D.A. 2017. Small scale habitat preferences of *Myotis daubentonii*, *Pipistrellus pipistrellus*, and potential aerial prey in an upland river valley // Acta Chiropterologica. Vol.19. P.255–272. DOI: 10.3161/15081109ACC2017.19.2.004

Twort V.G., Laine V.N., Field K.A., Whiting-Fawcett F., Ito F., Reiman M., Bartonicka T., Fritze M., Ilyukha V.A., Belkin V.V., Khizhkin E.A., Reeder D.M., Fukui D., Jiang T.L. & Lilley T.M. 2024. Signals of positive selection in genomes of Palearctic *Myotis*-bats coexisting with a fungal pathogen // BMC Genetics. Vol.25. Art.828. DOI: 10.1186/s12864-024-10722-3

Uzenbaeva L.B., Kizhina A.G., Ilyukha V.A., Belkin V.V. & Khizhkin E.A. 2019. Morphology and composition of peripheral blood cells during hibernation in bats (Chiroptera, Vespertilionidae) of northwestern Russia // Biology Bulletin. Vol.46. P.398–406. DOI: 10.1134/S1062359019030130

Vasen'kov D.A. & Potapov M.A. 2007. [Implementation of nutritional state index for the study of ecology of Chiroptera (Mammalia)] // Plecotus et al. No.10. P.21–31 [in Russian].

Vesterinen E.J., Ruokolainen L., Wahlberg N., Peña C., Roslin T., Laine V.N. & Lilley T.M. 2016. What you need is what you eat? Prey selection by the bat *Myotis daubentonii* // Moleclar Ecology. Vol.25. P.1581–1594. DOI: 10.1111/mec.13564

Vesterinen E.J., Puisto A.I.E., Blomberg A.S. & Lilley T.M. 2018. Table for five, please: dietary partitioning in boreal bats // Ecology and Evolution. Vol.8. P.10914–10937. DOI: 10.1002/ece3.4559

Virta M.E.T. 2014. Ectoparasites of Finnish bats and factors influencing parasite infestation levels. M.Sci. Thesis, University of Helsinki. 44 p.

Zahn A. & Rupp D. 2004. Ectoparasite load in European vespertilionid bats // Journal of Zoology. Vol.262. P.383–391. DOI: 10.1017/S0952836903004722