diversity

MDPI

Article

Ixodes apronophorus Schulze (Acari: Ixodida: Ixodidae): Distribution, Abundance, and Diversity of Its Mammal Hosts in West Siberia (Results of a 54-Year Long Surveillance)

Alfried V. Karimov [1], Natalia P. Korallo-Vinarskaya [1,2], Yulia F. Kuzmenko [1] and Maxim V. Vinarski [3,4,*]

1 Laboratory of Arthropod-Borne Viral Infections, Omsk Research Institute of Natural Foci Infections, 7 Mira Str., 644080 Omsk, Russia
2 Omsk State Pedagogical University, 14 Tukhachevskogo Emb., 644099 Omsk, Russia
3 Laboratory of Macroecology & Biogeography of Invertebrates, St. Petersburg State University, 7/9 Universitetskaya Emb., 199034 St. Petersburg, Russia
4 F.M. Dostoevsky Omsk State University, 11 Neftezavodskaya Str, 644053 Omsk, Russia
* Correspondence: radix.vinarski@gmail.com

Abstract: *Ixodes apronophorus* Schulze, 1924, the marsh tick, belongs to a group of so-called "neglected" ixodid ticks, which remain underexplored compared to the most well-studied species of the genus *Ixodes* (*I. ricinus*, *I. persulcatus*). In this communication, we analyze and summarize the quantitative data on the abundance of this parasite, its geographical distribution, and the diversity of its small mammal hosts in the region of West Siberia (Asiatic Russia). The analyzed data represent a continuous series of observations made between 1953 and 2007, which constitutes one of the longest timeseries ever studied by acarologists. It is shown that the marsh tick in West Siberia is most common in the northern forest steppe and southern taiga landscape zones, being distributed south of 60° N. Among 24 species of small mammals registered as hosts for *I. apronophorus* in the studied region, three play the most important role: the European water vole (*Arvicola amphibius*), the tundra vole (*Microtus oeconomus*), and the Northern red-backed vole (*Clethrionomys rutilus*). The data characterizing parasitism of the marsh tick on these three hosts in various landscape zones and subzones are provided. We can report a weak albeit significant negative relationship between the abundances of *I. apronophorus* and its small mammal hosts. The possible explanation lies in the mismatch between the cycles of abundance characteristic of the tick and its hosts.

Keywords: West Siberia; host–parasite relationships; the marsh tick; abundance cycles; Ixodidae

check for updates

Citation: Karimov, A.V.; Korallo-Vinarskaya, N.P.; Kuzmenko, Y.F.; Vinarski, M.V. *Ixodes apronophorus* Schulze (Acari: Ixodida: Ixodidae): Distribution, Abundance, and Diversity of Its Mammal Hosts in West Siberia (Results of a 54-Year Long Surveillance). *Diversity* **2022**, *14*, 702. https://doi.org/10.3390/d14090702

Academic Editor: Michael Wink

Received: 11 July 2022
Accepted: 18 August 2022
Published: 24 August 2022

1. Introduction

The epidemiological significance of the ixodid (hard) ticks (superfamily Ixodoidea; family Ixodidae) as vectors of numerous pathogenic agents is generally acknowledged. The family comprises around 700 species [1,2] and is cosmopolitan in its distribution [3]. Some representatives of the hard ticks (e.g., *Ixodes ricinus* (Linnaeus, 1758), *I. persulcatus* P. Schulze, 1930) have attracted enormous attention of researchers and, arguably, belong to the most-studied arthropod species. However, there is an apparent taxonomic bias in tick studies, with some species being relatively neglected by acarologists and parasitologists. *Ixodes* (*Ixodes*) *apronophorus* P. Schulze, 1924 (or the marsh tick), belongs to this group of "neglected" tick species [4], whose distribution, bionomics, association with mammal hosts, and epidemiological significance remain understudied. The number of publications devoted to this species is many times lower than the number of studies dealing with *I. ricinus* and *I. persulcatus* (Supplementary Information, Figure S1). This tick was described in Germany [5] and, subsequently, was recorded in many countries of West and Central Europe [4,6–10], West and Central Siberia [8,11–13], and Central Asia [8,14]. Sándor [15] provided an overview of the distribution of *I. apronophorus* as of 2017, with remarks on its life cycle and host preferences. Recently it was recorded in the Xinjiang Autonomous District of China [16], which, probably, constitutes the southernmost locality of this tick. It is a hygrophilous tick common in habitats with high humidity and situated close to waterbodies [3,8,12].

The main hosts for this parasite are the water vole *Arvicola amphibius* (Linnaeus, 1758), a rodent species broadly distributed in the north Palearctic, and the muskrat *Ondatra zibethicus* Linnaeus, 1766, with a Holarctic distribution [3,10]. Besides these mammal species, *I. apronophorus* can exploit a relatively broad range of hosts, including birds [8,11,13,15]. The only known case of an attack of the adult tick *I. apronophorus* on a human was reported by Fedorov [17].

Recently, several papers dealing with the morphology, phylogeny, ecology, and epidemiological significance of *I. apronophorus* have appeared (see [4,13,15] and references therein). Nonetheless, this species still belongs to a group of understudied tick species, which may have some practical implications, since *I. apronophorus* is known to serve as a vector of various infectious diseases of humans and animals, including tularemia, anaplasmosis, ehrlichiosis, borreliosis, and ricketsiosis [4,8,13,15,18]. The assumed role of the marsh tick in the spread of Omsk hemorrhagic fever [19,20] has recently been questioned [21].

The only comprehensive study of the marsh tick ecology in Siberia is that of Ivanov [22]. However, this research covered a rather restricted area within a single region of Russia, and no generalizations are possible based on Ivanov's data.

The shortage of data on the ecology of *I. apronophorus* hampers understanding of its potential role in the natural foci of infections, as well as the determination of the specificity of its associations with different host species. One of the possible ways to ameliorate this shortfall is to analyze large databases, collecting the primary data on occurrences, abundance, and host associations of particular parasitic species over substantial successions of years and extensive areas. The use of such databases accumulating results of long-term monitoring of blood-feeding arthropods allows us to address many questions of parasitology, biogeography of parasitism, and community ecology (see, for example, [23–26]).

In this communication, we discuss some peculiarities of abundance, distribution, population dynamics, and host association of *I. apronophorus* in the West Siberian Region, Russia. The analyzed information was taken from several archival sources containing data collected between 1953 and 2007, which constitutes one of the longest timeseries of ixodological observations available for such an analysis. Specifically, we aimed at studying the host range, distribution patterns, biotopes, and dynamics of abundance of *I. apronophorus* in West Siberia.

2. Material and Methods

The primary data for the analyses were taken from two archival databases containing records of sampling of various ixodid species in West Siberia (Figure 1). 1. The database of the Omsk Research Institute of Natural Foci Infections (Omsk, Russia) keeps data on occurrences of hard ticks and other ectoparasitic arthropods picked from small mammals and their nests during 1960–2007. In sum, it contains information on 14,491 small mammals, belonging to 31 rodent and nine shrew species, and 84 nests of various rodents and shrews (see [25] for a detailed description of this database). 2. The database of the Centre for Epidemiology and Hygiene of the Tyumen Region contains entries on 49252 small mammals and their ectoparasites collected between 1953 and 2007 in the Tyumen Region of Russia. In both cases, the primary data were taken by numerous collectors who were conducting the epidemiological monitoring of the natural foci of infections in West Siberia. The taxonomic identity of mammal hosts and their ectoparasites was determined shortly after collecting material in the field by experienced zoologists who worked in the two institutions mentioned above. The summarized research effort is equal to 90,585 traps/day. The paper cards from the two archives containing the data were digitized, and an electronic database was compiled in Microsoft Excel.

Figure 1. A map of the southern part of West Siberia with localities of *Ixodes apronophorus* taken from the analyzed archival databases.

In total, 11 species of hard ticks are represented in the database (in alphabetical order): *Dermacentor marginatus* (Sulzer, 1776), *D. reticulatus* (Fabricius, 1794), *D. silvarum* Olenev, 1931, *D. nuttalli* Olenev, 1928, *Haemaphysalis concinna* C. L. Koch, 1844, *Ixodes apronophorus* P. Schulze, 1924, *I. crenulatus* C.L. Koch, 1844, *I. lividus* C.L. Koch, 1844, *I. pavlovskyi* Pomerantsev, 1946, *I. persulcatus* P. Schulze, 1930, and *I. trianguliceps* Birula, 1895.

In the analyzed material, *Ixodes apronophorus* is represented by 7441 specimens picked from bodies of 2133 individual hosts; another 651 specimens of this tick were collected from small mammals' nests. All stages of the tick life cycle, i.e., adults, nymphs, and larvae, were used in the analyses. The bulk of the marsh tick specimens was collected from two regions of West Siberia—the Omsk Region (2959 exemplars) and the Tyumen Region (4250 exemplars); the rest of the ticks were collected from the territories of the Kemerovo, Novosibirsk, and Tomsk regions of Russia (all situated in West Siberia). However, we did not use the administrative regions as the primary units of analysis; instead, we studied the distribution of *I. apronophorus* among the three main landscape zones of West Siberia (forest, forest steppe, and steppe), with the forest and forest steppe zones being subdivided in several subzones (in accordance with the zonation of Rikhter [27]). The particular groups of the biotopes within the landscape zones (subzones) were identified chiefly on the basis of their dominant vegetation (i.e., sphagnum mires, birch groves, meadows, etc.). However, this vegetation-based classification could not be applied consistently, and some biotope groups were defined on other grounds. For example, we used the term 'ecotone' to designate a border-line locality, which cannot be placed unequivocally to either of the two adjacent types. The 'anthropogenic biotope' category was applied to a variety of localities transformed, to some extent, by intense human activity; most often, such biotopes were situated within small settlements and villages. Lastly, we united wetlands and floodplain stations in a single group of periaquatic habitats, irrespective of what type of vegetation they have. In total, 22 biotope groups were discerned. We fully realize that such a classification is crude and artificial, and we used it as a means of the primary arrangement of a plethora (>180) of concrete biotopes sampled by different workers during more than 50 years. In any case, the primary data contained in the two analyzed databases are not accompanied by a more or less complete description of the vegetation, which would allow us to consistently classify the studied biotopes on a phytocoenological basis.

A set of indices characterizing different aspects of tick parasitism on small mammals were applied [28–30].

The index of abundance (I_A) is calculated as the average number of parasites of a given species per host or nest [28]. The index of dominance (I_D) is defined as the ratio between the number of *I. apronophorus* individuals collected from a given host species to the number of all ixodid ticks collected from this host. Usually, it is expressed as a fraction of 100%. The relative index of dominance, expressed in points, 1 to 5, allows one to estimate a commonness (or, alternatively, rarity) of a given species in a given region [28]. The points have the following verbal characteristics: 5 (dominant), 4 (subdominant), 3 (frequent), 2 (subfrequent), and 1 (rare). See Table S1 in Supplementary information for details.

For the identification of the principal mammal hosts for *I. apronophorus* in West Siberia, Pesenko's index of relative host fidelity (I_P) was used. The calculation of this index is as follows [29]:

$$Ip = \frac{n' \times N - n \times N'}{n' \times N + n \times N' - 2n' \times N'}, \text{ where} \tag{1}$$

n—amount of *I. apronophorus* individuals collected from all host mammals;
n′—amount of *I. apronophorus* individuals collected from a given host mammal;
N—amount of all ixodid individuals collected from all host mammals;
N′—amount of all ixodid individuals collected from a given host mammal.

The values of Pesenko's index can vary from −1 to +1. The values > + 0.31 indicate the significant fidelity of a parasite species to its host species; the values lying between +0.30 and −0.30 shows neutrality, and the values below −0.31 correspond to accidental findings of a parasite species on this host (no interaction altogether) (see [29] for details). I_P = 1 corresponds to a case when a parasite species is found in the only host species. The choice of these indices was determined by their use in the Soviet and Russian parasitological literature, which secures the comparability of our data with those published by the Russian authors who studied other ixodid species, i.e., *I. persulcatus* (see Filippova [31] for a detailed review of the ecology of this species).

We calculated the so-called *hostal–topical index* (I_{HT}), proposed relatively recently by Bogdanov et al. [30], as an integrated measure of a parasite's relationship with its host and biotope. (Pesenko's index can reveal the relationship of a parasite with either its host or its biotope, but not simultaneously with both variables.) This index is calculated as:

$$I_{HT} = \frac{n}{N} - \frac{n_1}{N_1} \times \frac{n_2}{N_2}, \tag{2}$$

where

n—amount of *I. apronophorus* individuals collected from a given host species in a given biotope;
N—amount of all ixodid individuals collected from a given host species in a given biotope;
n_1—amount of host indiduals of *I. apronophorus* collected in a given biotope;
N_1—amount of host individuals of all ixodid ticks collected in a given biotope;
n_2—amount of *I. apronophorus* individuals collected from all hosts in a given biotope;
N_2—amount of individuals of all ixodid ticks collected in a given biotope.

The values of this index equal to or exceeding 0.50 correspond to the significant relationship of a parasite with a given host species, whereas the values <0.10 indicate the significant relationship with biotope (not with host). The intermediate values, 0.10 < I_{HT} < 0.50, mean that both biotope and host identity influence the abundance of a given parasite species [30].

To study the temporal changes in marsh tick abundance, we chose a subset of the primary database which contains data collected in a continuous sequence of years, between 1962 and 2007, in the Tyumen Region, by the same collector (A.P. Zuevsky, Tyumen). The subset includes entries of about 3031 host individuals, from which 1350 individuals of *I. apronophorus* were picked. The total sampling effort was equal to 16,871 trap/days. The sampling area is situated within three landscape zones: northern forest steppe, aspen–birch forests, and southern taiga. The abundance of mammal hosts was expressed as number of sampled individuals per 100 trap/days, whereas for ticks the values of I_A were used. To reveal a possible cyclicity in the dynamics of the abundance of small mammals and ticks, the spectral (Fourier) analysis of time series was applied. This is a standard statistical method enabling researchers to detect cyclicity and determine the variance in the data accounted for by cyclic activity. The essentials of this method can be found elsewhere [32–34]. Maximov and Erdakov [35] were the first authors to apply the spectral analysis to the study of cyclicity in abundance of small mammals in West Siberia. We generally follow here the approach used in their monograph.

Statistical calculations were performed in MS Excel for Windows and STATISTICA 12.0 (StatSoft Inc., Tulsa, Oklahoma, USA). The mapping of the marsh tick occurrences was made utilizing QGIS 3.0 software based on geographical coordinates of localities sampled between 1953 and 2007.

3. Results

Ixodes apronophorus was recorded in several landscape zones and subzones of West Siberia, being distributed between 53 and 60° N (see Figure 1). The southern limit of this species in the region is unknown but the tick certainly occurs to the south of the 54th latitude, since its findings in the Altai Region of Russia, situated south of the area covered by our database, are known [8,36]. The marsh tick occurrences registered north of the 58th latitude are rather scarce (see Figure 1). *I. apronophorus* occurs in all landscape zones and subzones represented within the studied area (Table 1).

The calculations of the relative index of dominance of the marsh tick in West Siberia have shown this species is dominant (5 points) in the subzones of southern taiga, aspen–birch forests and the northern forest steppe. The values of the relative abundance of the species of 4 points (subdominant) were found in the submontane forest steppe. In the aspen–fir taiga and montane taiga subzones, *I. apronophorus* is subfrequent (2 points), and in the middle taiga and steppe it is rare (1 point).

According to our data, the host range of *Ixodes apronophorus* in West Siberia includes 24 species of small and medium-sized mammals belonging to the three orders: Eulipotyphla, Rodentia, and Lagomorpha (see Table 1). The highest diversity of hosts of *I. apronophorus* is observed in the southern taiga, aspen–birch forests, and northern forest steppe subzones. The relative importance of different mammal species as hosts of the marsh tick in West Siberia is, however, sharply uneven. Even though the highest values of the index of abundance were found in *Neomys fodiens* and *Sorex minutus* (see Table 1), these two mammals cannot be considered principal hosts for *I. apronophorus* throughout the studied area, and their pronounced interactions with the parasite are observed in a few landscape zones only.

The circle of the true principal hosts, determined in accordance with Pesenko's index, is much narrower and includes only six species of small mammals. The significant values of the I_P index were obtained for only a few host species in four landscape zones, which are characterized by the largest sampling effort (Table 2). The values of this index for the rest of the cases were either neutral or negative and, hence, are not reported in Table 2. Among the six mammal species included in this table, we consider the three insectivores, *Neomys fodiens*, *Sorex araneus*, and *S. minutus*, as subprincipal hosts of the marsh tick in West Siberia, since the former species is abundant only in a single landscape zone (northern forest steppe; see Table 1), while the two latter ones demonstrate rather low values of I_a throughout the studied area. Thus, the principal hosts for *I. apronophorus* in West Siberia, according to the criteria we followed, are the European water vole (*Arvicola amphibius*), the tundra vole (*Microtus oeconomus*), and the Northern red-backed vole (*Clethrionomys rutilus*). This result was proved using the index of dominance, as the independent source of data on the relative significance of particular mammal species as hosts for the marsh tick (Table S2 in Supplementary Materials). All species identified by us as principal or subprincipal hosts of *I. apronophorus* belong to the group of host species with the highest values of I_D. We restricted our subsequent analyses to the three principal host species only.

Table 1. Mammal hosts of *Ixodes apronophorus* in West Siberia and their presence/absence in different landscape zones and subzones, with the values of their respective I_A. Host species are arranged according to their mean I_A values (in descending order).

Host Species	Mean I_A	Landscape Zone/Subzone								
		Forest					Forest Steppe			Steppe
		Middle Taiga	Southern Taiga	Aspen−Birch Forests	Aspen−Fir Taiga	Montane Taiga	Northern	Southern	Submontane	
Neomys fodiens (Pennant, 1771)	0.79	–	+ *	+	–	–	0.79	–	+	–
Sorex minutus Linnaeus, 1766	0.68	–	1.75	+	–	–	0.15	–	+	–
Microtus agrestis (Linnaeus, 1761)	0.48	–	0.93	+	+	+	0.02	–	(0.06)	–
Sorex daphaenodon Thomas, 1907	0.45	–	0.42	–	–	+	0.48	–	+	–
Arvicola amphibius (Linnaeus, 1758)	0.43	0.07	0.27	0.42	+	–	0.61	–	+	0.10
Clethrionomys rutilus (Pallas, 1779)	0.35	+	0.42	0.58	+	+	0.15	+	0.05	+
Microtus oeconomus (Pallas, 1776)	0.32	+	0.20	0.86	0.06	+	0.22	–	0.08	+
Cricetus cricetus (Linnaeus, 1758)	0.29	–	–	+	+	–	0.29	–	+	–
Clethrionomys glareolus (Schreber, 1780)	0.28	+	0.49	0.25	+	+	0.08	–	0.06	–
Sorex tundrensis Merriam, 1900	0.26	–	+	–	–	–	0.26	–	–	–
Sorex araneus Linnaeus, 1758	0.22	+	0.27	0.22	+	+	0.24	+	0.15	–
Microtus gregalis (Pallas, 1779)	0.19	–	+	0.07	–	–	0.23	+	+	+
Microtus arvalis (Pallas, 1779)	0.20	–	+	0.09	–	–	0.31	–	–	–
Apodemus agrarius (Pallas, 1771)	0.12	–	0.12	0.15	+	+	0.04	+	0.02	+
Sylvaemys uralensis (Pallas, 1811)	0.08	–	–	+	+	–	+	+	0.08	–
Eutamias sibiricus (Laxmann, 1769)	0.10	+	+	+	+	–	+	–	0.10	–
Sicista betulina (Pallas, 1778)	0.11	–	–	+	–	+	0.14	–	0.07	–
Clethrionomys rufocanus (Sundevall, 1846)	0.06	–	0.05	0.13	0.02	+	0.08	–	–	+
Ondathra zibetica (Linnaeus, 1766)	0.01	–	–	+	–	–	0.01	–	–	–
Lepus timidus Linnaeus, 1758	–	–	+	+	–	–	+	+	–	–
Rattus norvegicus (Berkenhout, 1769)	–	–	–	+	–	–	+	–	–	–
Sorex arcticus Kerr, 1792	–	–	+	+	+	–	+	–	+	–
Sorex caecutiens Laxmann, 1788	–	–	+	–	–	+	+	–	–	–
Sorex isodon Turov, 1936	–	–	+	+	–	–	–	–	–	–

* The values of I_a are not calculated due to the limited sample of the host individuals in this zone/subzone (n ≤ 10).

Table 2. Positive values of I_P (≥0.31) calculated for different host species of *I. apronophorus* in different landscape zones (subzones) of West Siberia.

Host Species	Landscape Zone/Subzone			
	Middle Taiga	Southern Taiga	Aspen–Birch Forests	Northern Forest Steppe
Arvicola amphibius	0.49	0.99	0.53	0.79
Clethrionomys rutilus	n/a	n/a	0.52	n/a
Microtus oeconomus	n/a	0.52	0.33	0.49
Neomys fodiens	n/a	n/a	n/a	0.63
Sorex araneus	n/a	n/a	n/a	0.31
Sorex minutus	n/a	n/a	n/a	0.39

The three principal hosts demonstrate great variability in their interactions with *I. apronophorus*, which (partially) depends on habitat. The significant values of I_{HT} were found in a limited number of analyzed biotopes, and each principal host species shows a unique relationship pattern with the marsh tick (Table 3). The red-backed vole seems not to form strong interactions with *I. apronophorus*, and the type of biotope determines the abundance of this tick in the majority of biotopes (in most cases, the I_{HT} values are lower than 0.10; see Table 3). On the other hand, both *Arvicola amphibius* and *Microtus oeconomus* tend to form tight relationships with the marsh tick, especially in humid and semi-humid biotopes—*Sphagnum* mires, meadows, and various localities united under the 'periaquatic habitats' label (see Table 3). No common tendency in the parasitizing of three host species by the marsh tick, which would be consistent through the landscape zones (subzones) of West Siberia, can be reported.

Table 3. Values of I_{HT} calculated for *I. apronophorus* in different biotope groups in West Siberia. The values showing the significant relationship with the host (>0.50) are given in bold.

Landscape Zone/Subzone	Biotope Group	Host Species		
		M. oeconomus	*A. terrestris*	*C. rutilus*
Middle Taiga	periaquatic habitats	n/a	0.490	n/a
	coniferous and mixed forests	n/a	n/a	0.013
Southern taiga	deciduous forests	n/a	n/a	0.005
	periaquatic habitats	**0.800**	**0.650**	−0.261
	aspen–birch groves	n/a	n/a	0.222
	aspen groves	n/a	n/a	0
	Sphagnum mires	**0.854**	**0.869**	0.354
	coniferous and mixed forests	0.272	n/a	0.025
	ecotones	n/a	n/a	0.214
Aspen–birch forests	birch–aspen groves	**0.995**	n/a	−0.004
	birch groves	n/a	n/a	0.147
	linden forests	n/a	n/a	0.038
	deciduous forests	**0.713**	**0.927**	0.109
	meadows	**0.932**	**0.682**	0.124
	periaquatic habitats	0.485	**0.550**	−0.150
	aspen–birch groves	**0.849**	n/a	n/a
	Sphagnum mires	**0.711**	**0.710**	0.192
	reed beds	0.000	0.250	n/a
	coniferous and mixed forests	n/a	n/a	0.100
	ecotones	n/a	**0.90**	0.162

Table 3. *Cont.*

Landscape Zone/Subzone	Biotope Group	Host Species		
		M. oeconomus	*A. terrestris*	*C. rutilus*
Aspen–fir taiga	coniferous and mixed forests	0.014	n/a	n/a
Northern forest steppe	aspen–birch groves	n/a	n/a	0.423
	birch groves	–0.178	0.291	−0.222
	deciduous forests	0.345	n/a	0.024
	meadows	0.473	n/a	**0.518**
	periaquatic habitats	0.197	**0.510**	−0.073
	Sphagnum mires	n/a	**0.922**	n/a
	coniferous and mixed forests	0.094	**0.983**	−0.003
	ecotones	**0.749**	n/a	0.026
Submonate forest steppe	coniferous and mixed forests	0.028	**0.585**	−0.006
Steppe	dry fescue–feather grass steppe	n/a	**0.998**	n/a

An attempt to find any clear relationship between the abundance of mammal hosts and the marsh tick in the Tyumen region, based on a 46-year-long sequence of data (1962–2007), produced a diagram showing that there is no strict coincidence between the peaks of abundance of *I. apronophorus* and that of its small mammal hosts (Figure 2). In most cases, the abundance peaks in these two groups took place in different years, with a few exceptions (2002; see Figure 2). Sometimes, as in 1968 and 1989, the abundance peak of *I. apronophorus* coincided with a marked depression of populations of small mammals. Rather surprisingly, a weak but statistically significant negative correlation (Spearman's correlation coefficient = −0.36; p = 0.015) between the two timeseries was found. We were unable to reveal any significant correlation either when nymphs and larvae of the marsh tick were analyzed separately or when the abundance of the three principal hosts was considered individually (results not shown). Thus, there is no plain relationship between the abundances of *I. apronophorus* and its mammal hosts in the studied area.

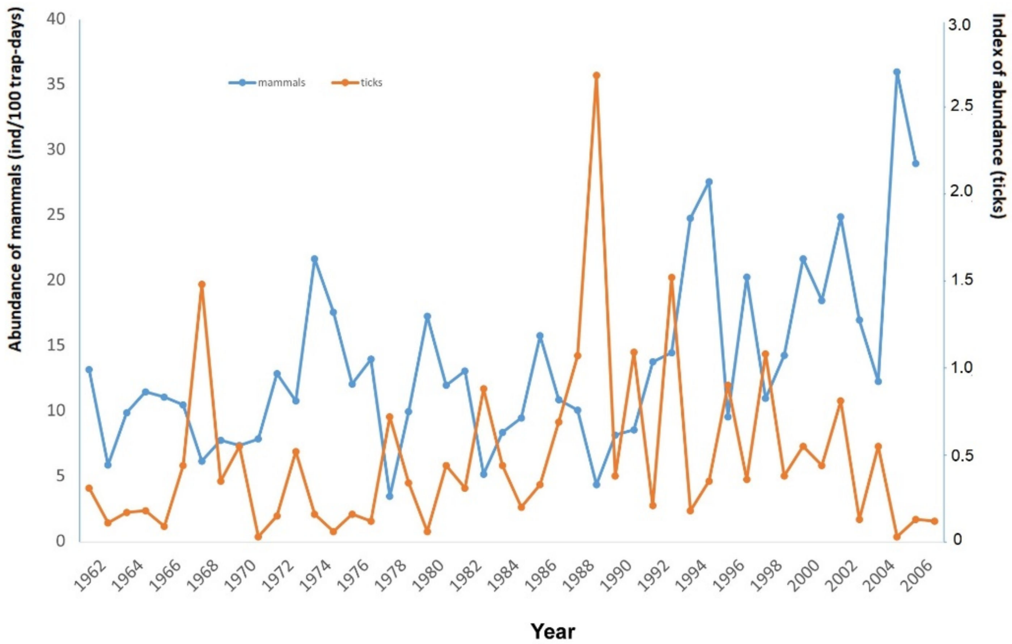

Figure 2. The dynamics of abundance of *Ixodes apronophorus* and its mammal hosts in West Siberia.

Spectral analysis of the timeseries shows that the abundance of small mammals in Tyumen Region shows two cycles of fluctuations, a shorter cycle, with a period of approximately 2.70 years, and a longer one, with a duration of 6.60 years (Figure 3A). Another, much longer cycle of abundance fluctuations equal approximately to 23 years (i.e., multiple to the mean value of the two shorter cycles) can be traced as well (see Figure 3A).

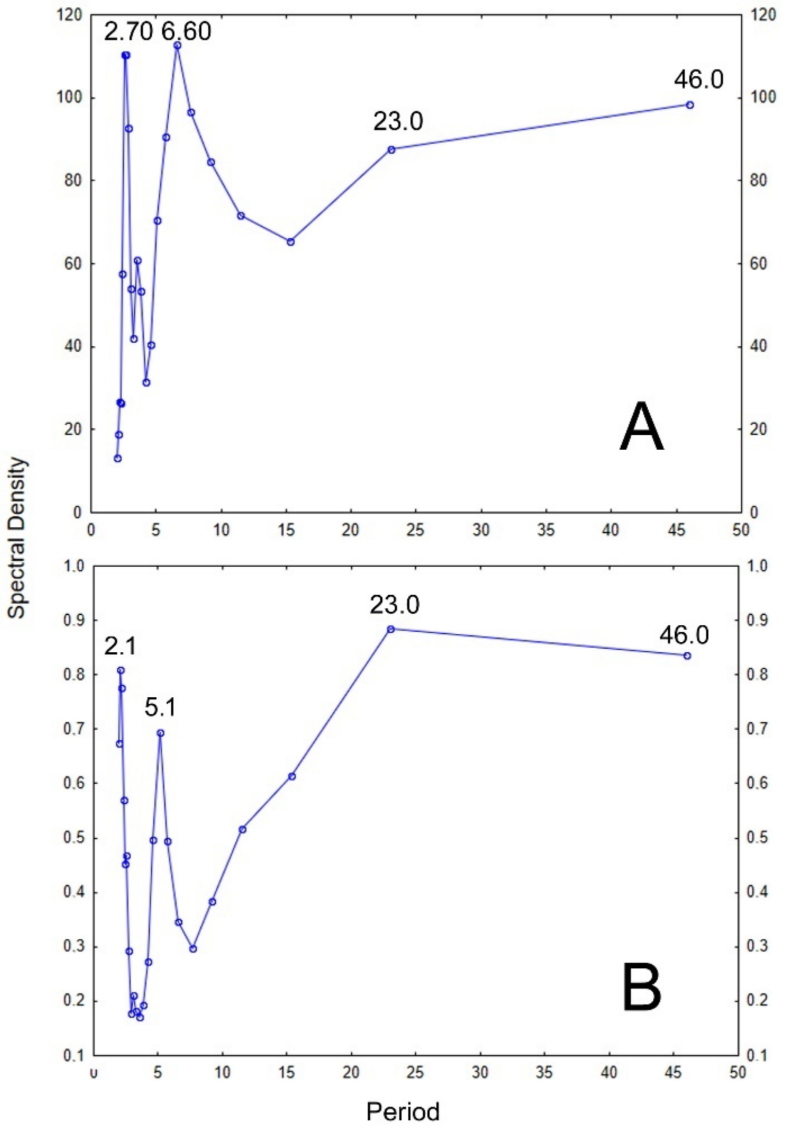

Figure 3. Results of spectral analysis of two timeseries: (**A**) The abundance of small mammals in the Tyumen Region, 1962–2007; (**B**) The index of abundance of *I. apronophorus* in the same area, 1962–2007. Both graphs are based on the relative, not absolute, measures of abundance.

Despite the overall similarity between the patterns of dynamics of the marsh tick and that of its mammal hosts, there is a significant time lag between the peak abundances of these groups equal, roughly, to 4–6 years (Figure 4).

The dynamics of abundance of *I. apronophorus* demonstrates a similar picture, but the periods of abundance cycles are somewhat different. Two shorter cycles, with periods of 2.09 and 5.11 years, can be discerned, as well as a longer cycle of abundance fluctuations which is equal to 23 years (Figure 3B). The latter is apparently analogous to the longest cycle of abundance found in small mammals and, possibly, represents a statistical artefact.

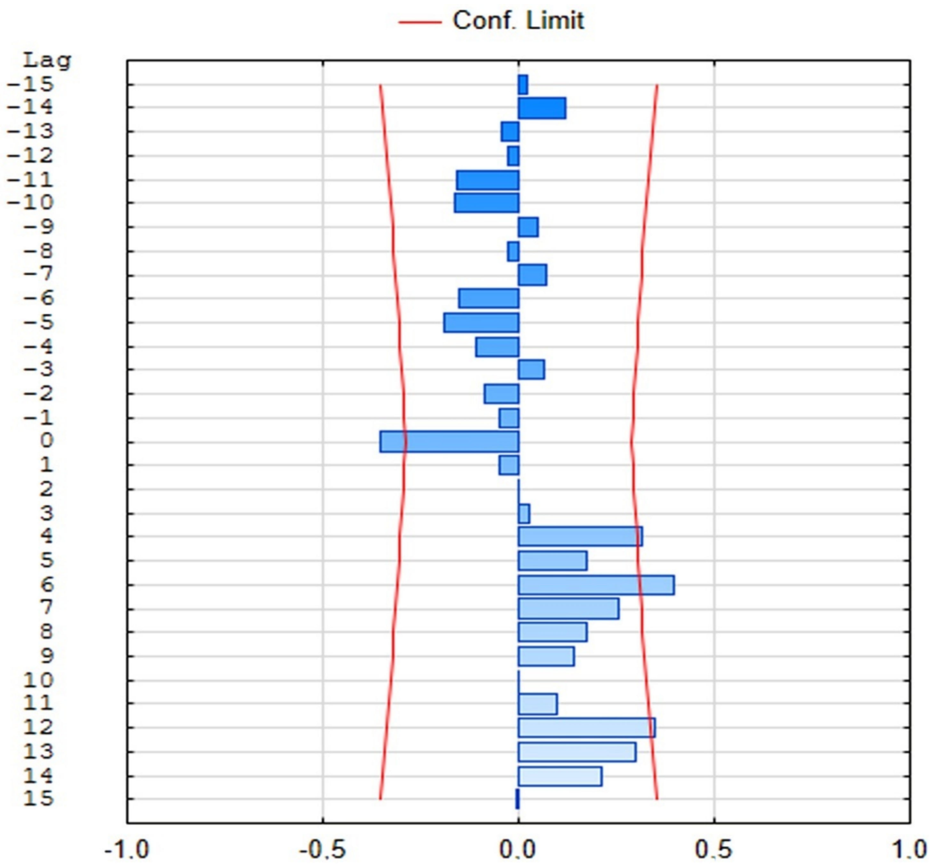

Figure 4. Cross-correlation of the abundance of *Ixodex apronophorus* and its mammal hosts in the Tyumen Region, West Siberia.

4. Discussion

Generally, the obtained results fit the data on the ecology of *I. apronophorus* available from the literature well. The novelty of our research lies in a study of a rather long (54 years) period of surveillance and in an attempt to analyze the abundance dynamics of the marsh tick as being possibly influenced by the abundance of its mammal hosts. The overall circle of mammals parasitized by *I. apronophorus* in West Siberia includes approximately 40 species [12,21]; however, a significant portion of these mammals do not serve as reliable hosts of this tick. For example, the findings of *I. apronophorus* on bodies of small carnivores (mustelids) must be considered as accidental. Most authors regard the European water vole as the main host of the marsh tick in the region [21,22,37], which corresponds well with our results. However, the abundance of this species in most parts of its range is prone to drastic interannual fluctuations, with periodic outbreaks followed by precipitous declines [37–42]. According to Formozov's data, collected in the Volga Delta [43], in some years, wild boars become much more common there than water voles. The same is generally characteristic to the West Siberian population of this rodent [37].

Remarkably, the peaks of the *A. amphibius* abundance in the south of West Siberia (the Baraba steppe), as revealed by spectral analysis, have periods of 2.7, 4.0, and 8.0 years [38]; the first value is identical to that obtained during this research. In our opinion, due to these fluctuations, populations of *I. apronophorus* in West Siberia must rely on the presence of alternative principal hosts, other than *Arvicola amphibius*. For example, in some regions of Siberia, the tundra vole can replace *A. amphibius* in the years of its population depression. According to our observations, the tundra vole serves as the second most important host for the marsh tick in the studied region, whereas the role of *C. rutilus* seems to be less important in most landscape zones/subzones.

Another explanation of the existence of the principal hosts of the marsh tick other than *A. amphibius*, is that the water vole is a rather stenotopic rodent, adapted to dwell in periaquatic habitats and even characterized as "endemic to the floodplains" [41].

Ecologically, the majority of host species of the marsh tick (*A. amphibius*, *M. oeconomus*, *N. fodiens*) prefer to live in habitats with increased humidity; the red-backed vole is a generalist species that also tends to avoid relatively dry environments. The very vernacular name of this parasite (the marsh tick) emphasizes its tendency to dwell in relatively wet habitats [15,44]. The potential role of the *Sorex* shrews as hosts for the marsh tick deserves further investigation; our results show that this role can be significant in some landscape zones of West Siberia (see also [13]).

The weak negative relationship between the abundances of *I. apronophorus* and its mammal hosts is by no means surprising; the same phenomenon was observed for the taiga tick, *I. persulcatus*, in different parts of its range in Northern Asia [31], and some other tick species in Europe [45]. A similar situation was reported in some other case studies: fleas parasitizing *Apodemus* mice in Slovakia [46], ticks and fleas collected from small mammals in Scotland [47], etc. A plausible explanation for this negative correlation is based on the so-called "dilution effect", i.e., as the host abundance increases, the parasites are divided between more potential hosts and, hence, individual hosts are less likely to be infested [46,47]. According to Krasnov et al. [46], the dilution effect is better expressed in generalist tick species than in ecological specialists, i.e., those species that are adapted to infest the only or a few hosts. Our results fit with this prediction, since *I. apronophorus* can be classified as a generalist rather than a specialist parasite (see Results).

However, it seems that there is no common tendency, since in some regions no significant correlation, either positive or negative, was found (see Filippova [31]; the data on *Ixodes persulcatus*). The negative tendency can be cautiously explained by a hypothesis that the increase in the tick abundance follows the increase in its host numbers, lagging behind the latter by 1–2 years. Our results show that the lag may be even broader and constitute 4–6 years (see Results). In general, the mismatch between the periods of abundance fluctuations of the marsh tick and its hosts produces the mismatch in their abundance peaks and, as a consequence, the visible discrepancy between the two timeseries (see Figure 2). A similar discrepancy is quite characteristic of the taiga tick, the most well-studied ixodid species in Siberia [31].

The results and discussions presented above depict *I. apronophorus* as a relatively oligohostal (i.e., it has a few principal hosts), moisture-loving, and moderately abundant West Siberia tick species. Despite this parasite having a secondary epidemiological significance in the region, compared to *I. persulcatus*, it is more or less widely distributed, able to dwell in a variety of stations, and exploits a number of small mammal hosts, both principal and secondary.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14090702/s1, Figure S1. Number of articles dealing with various species of *Ixodes* of Europe and Northern Asia. Based on a Web of Science search using the article titles and keywords (assessed on 22 October 2021). Abbreviations: *Iric—Ixodes ricinus*; *Iper—I. persulcatus*; *Ihex—I. hexagonus*; *Itri—I. trainguliceps*; *Ipav—I. pavlovskyi*; Iliv—*I. lividus*; *Iapr—I. apronophorus*; *Icre—I. crenulatus*. Table S1. The method of calculation of the relative dominance of *Ixodes apronophorus* (modified after Pesenko [29]). The relative abundance is expressed in points, 1 to 5, whose verbal characteristics are given in the main text. Table S2. The mean values of ID (in %) of *I. apronophorus* in different landscape zones/subzones of West Siberia.

Author Contributions: Conceptualization, A.V.K. and M.V.V.; Methodology, A.V.K., N.P.K.-V. and M.V.V.; Software, M.V.V.; Validation, M.V.V.; Lab work A.V.K., Y.F.K. and N.P.K.-V.; Database Preparation, A.V.K. and Y.F.K.; Statistical Analysis, A.V.K. and M.V.V.; Writing—Original Draft Preparation, A.V.K. and M.V.V.; Writing—Review and Editing, all authors; Visualization, M.V.V.; Supervision, N.P.K.-V. and M.V.V.; Project Administration, M.V.V. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The primary data for this study are available from the authors upon request.

Acknowledgments: The authors are grateful to their colleagues: Igor I. Bogdanov (Omsk), Zhanna S. Tyulko (Omsk), and Marat T. Makenov (Moscow) for their help and advice received during this research.

Conflicts of Interest: The authors declare no conflict of interests.

References

1. Keirans, J.E. Order Ixodida. In *A Manual of Acarology*; Krantz, G.W., Walter, D.E., Eds.; Texas Tech University Press: Lubbock, TX, USA, 2009; pp. 111–123.
2. Nava, S.; Guglielmone, A.A.; Mangold, A.J. An overview of systematics and evolution of ticks. *Front. Biosci.* **2009**, *14*, 2857–2877. [CrossRef] [PubMed]
3. Kolonin, G.V. *World Distribution of Ixodid Ticks (Genus Ixodes)*; Nauka Publishers: Moscow, Russia, 1981. (In Russian)
4. Andersson, M.O.; Radbea, G.; Frangoulidis, D.; Tomaso, H.; Rubel, F.; Nava, S.; Chitimia-Dobler, L. New records and host associations of the tick *Ixodes apronophorus* and the first detection of *Ehrlichia* sp. HF in Romania. *Parasitol. Res.* **2018**, *117*, 1285–1289. [CrossRef] [PubMed]
5. Schulze, P. *Ixodes apronophorus* n. s. eine neue deutsche Zecke von *Arvicola amphibius* L. *Zool. Anz.* **1924**, *59*, 281–284.
6. Feider, Z. *Fauna of the People's Republic of Romania. Suprafamily Ixodoidea. Ticks*; The Academy of Sciences of the Romanian People's Republic Press: Bucharest, Romania, 1965. (In Romanian)
7. Gilot, B.; Moncada, E.; Pautou, G. Presence in France d'*Ixodes apronophorus* (Schulze, 1924). Ixodoidea—Ixodidae. *Ann. Parasit.* **1976**, *51*, 601–603. [CrossRef]
8. Filippova, N.A. Ixodid ticks of the subfamily Ixodinae. *Fauna SSSR Paukoobraznyye* **1977**, *4*, 1–396. (In Russian)
9. Nowak-Chmura, N.; Siuda, K. Ticks of Poland. Review of contemporary issues and latest research. *Ann. Parasitol.* **2012**, *58*, 125–155.
10. Stanko, M.; Derdáková, M.; Špitalská, E.; Kazimírová, M. Ticks and their epidemiological role in Slovakia: From the past till present. *Biologia* **2022**, *79*, 1575–1610. [CrossRef]
11. Voltsit, O.V. New faunistic records of the ixodid ticks from eastern regions of Russia in collections of the Zoological Museum of the Moscow State University. Description of the nymph of *Ixodes* (*Monoindex*) *maslovi*. *Parazitologiya* **1997**, *31*, 265–268. (In Russian)
12. Yakimenko, V.V.; Malkova, M.G.; Shpynov, S.N. *Ixodid Ticks of the Western Siberia*; Omskiy Nauchnyi Vestnik: Omsk, Russia, 2013. (In Russian)
13. Rar, V.; Yakimenko, V.; Tikunov, A.; Vinarskaya, N.; Tancev, A.; Babkin, I.; Epikhina, T.; Tikunova, N. Genetic and morphological characterization of *Ixodes apronophorus* from Western Siberia, Russia. *Ticks Tick-Borne Dis.* **2020**, *11*, 101284. [CrossRef]
14. Galuzo, I.G. *Blood-Feeding Acari of Kazakhstan. Vol. IV. Genus Boophilus Curlice, 1891. Genus Haemaphysalis Koch, 1844. Genus Ixodes Latreille, 1795*; The Kazakh SSR Academy of Sciences Press: Alma-Ata, Kazakhstan, 1949. (In Russian)
15. Sándor, A. Ixodes apronophorus Schulze, 1924. In *Ticks of Europe and North Africa*; Estrada-Peña, A., Mihalca, A., Petney, T., Eds.; Springer: Cham, Switzerland, 2017; pp. 179–181.
16. Guo, Y.; Sun, Y.; Xu, R. The genus *Ixodes* (Acari: Ixodidae) in China with three new record species. *Acta Parasitol.* **2016**, *61*, 729–742. [CrossRef]
17. Fedorov, V.G. Ixodoidea ticks on humans in western Siberia. *Meditsinskaya Parazitol. Parazit. Bolezn.* **1968**, *37*, 615–616. (In Russian)
18. Igolkina, Y.P. Molecular Genetic Analysis of Rickettsiae Circulating in Siberia and the Far East. Ph.D. Thesis, Institute of Chemical Biology and Fundamental Medicine, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia, 2019. (In Russian)
19. Kharitonova, N.N.; Leonov, Y.A. *Omsk Haemorrhagic Fever*; Nauka Publishers: Novosibirsk, Russia, 1978. (In Russian)
20. Lvov, D.K. Omsk hemorrhagic fever. In *The Arboviruses: Epidemiology and Ecology*; Monath, T.P., Ed.; CRC Press: Boca Raton, FL, USA, 1988; Volume 3, pp. 205–216.
21. Yakimenko, V.V.; Malkova, M.G.; Tyulko, Z.S.; Morozova, O.V. *Vector-Borne Viral Infections of Western Siberia (Regional Aspects of Epidemiology, Ecology of Pathogens and Issues of Microevolution)*; KAN: Omsk, Russia, 2019. (In Russian)
22. Ivanov, D.I. The Tick *Ixodes apronophorus* P. Sch., Some Features of Its Ecology and Epizootic Significance in the Natural Foci of Tularemia in the Northern Forest-Steppe of Omsk Region. Ph.D. Thesis, Biological Institute, Siberian Branch of the Soviet Academy of Sciences, Novosibirsk, Russia, 1975. (In Russian)
23. Krasnov, B.R.; Vinarski, M.V.; Korallo-Vinarskaya, N.P.; Mouillot, D.; Poulin, R. Inferring associations among parasitic gamasid mites from census data. *Oecologia* **2009**, *160*, 175–185. [CrossRef]
24. Krasnov, B.R.; Matthee, S.; Lareschi, M.; Korallo-Vinarskaya, N.P.; Vinarski, M.V. Co-occurrence of ectoparasites on rodent hosts: Null model analyses of data from three continents. *Oikos* **2010**, *119*, 120–128. [CrossRef]

25. Krasnov, B.R.; Vinarski, M.V.; Korallo-Vinarskaya, N.P.; Shenbrot, G.I.; Khokhlova, I.S. Species associations in arthropod ectoparasite infracommunities are spatially and temporally variable and affected by environmental factors. *Ecol. Entomol.* **2021**, *46*, 1254–1265. [CrossRef]
26. van der Mescht, L.; Warburton, E.M.; Khokhlova, I.S.; Stanko, M.; Vinarski, M.V.; Korallo-Vinarskaya, N.P.; Krasnov, B.R. Biogeography of parasite abundance: Latitudinal gradient and distance decay of similarity in the abundance of fleas and mites, parasitic on small mammals in the Palearctic, at three spatial scales. *Int. J. Parasitol.* **2018**, *48*, 857–866. [CrossRef]
27. Rikhter, G.D. (Ed.) *West Siberia*; The Soviet Academy of Sciences Press: Moscow, Russia, 1963. (In Russian)
28. Beklemishev, V.N. Terms and concepts needed for the quantitative study of populations of ectoparasites and nidicolous species. *Zool. Zh.* **1961**, *40*, 149–158. (In Russian)
29. Pesenko, Y.A. *The Principles and Methods of Quantitative Analysis in Faunal Studies*; Nauka Publishers: Moscow, Russia, 1982. (In Russian)
30. Bogdanov, I.I.; Chachina, S.B.; Korallo, N.P.; Dmitriev, V.V. A new parasitological index for the estimation of peculiarities of the relationships between parasite and its host, and biotope of the host. *Parazitologiya* **2006**, *40*, 105–112. (In Russian)
31. Filippova, N.A. (Ed.) *Taiga Tick Ixodes Persulcatus Schulze (Acarina, Ixodidae). Morphology, Systematics, Ecology, Medical Importance*; Nauka Publishers: Moscow, Russia, 1985. (In Russian)
32. Thomas, K.A. Time-series analysis—Spectral analysis and the search for cycles. *West. J. Nurs. Res.* **1990**, *12*, 558–562. [CrossRef]
33. Bloomfield, P. *Fourier Analysis of Time Series. An Introduction*; John Wiley & Sons: New York, NY, USA, 2000.
34. Anderson, T.W. *The Statistical Analysis of Time Series*; John Wiley & Sons: Hoboken, NJ, USA, 2011.
35. Maximov, A.A.; Erdakov, L.N. *The Cyclical Processes in Animal Communities (Biorhythms, Successions)*; Nauka Publishers, Siberian branch: Novosibirsk, Russia, 1985. (In Russian)
36. Netsky, G.I.; Alifanov, V.I.; Bogdanov, I.I.; Gorelova, N.B. To the study of the fauna and distribution of ixodid ticks in Western Siberia in relation to their role in the natural foci of some infections. In *Pervoyye Akarologicheskoye Soveshchaniye*; Tezisy Dokladov: Moskva-Leningrad, Russia, 1966; pp. 146–147. (In Russian)
37. Panteleyev, P.A. (Ed.) *The Water Vole: An Image of the Species*; Nauka Publishers: Moscow, Russia, 2001. (In Russian)
38. Maximov, A.A. *Nature's Cycles: The Causes of the Recurrence of Ecological Processes*; Nauka: Leningrad, Russia, 1989. (In Russian)
39. Fichet-Calvet, E.; Pradier, B.; Quéré, J.P.; Giraudoux, P.; Delattre, P. Landscape composition and vole outbreaks: Evidence from an eight-year study of *Arvicola terrestris*. *Ecography* **2000**, *23*, 659–668. [CrossRef]
40. Cerqueira, D.; De Sousa, B.; Gabrion, C.; Giraudoux, P.; Quéré, J.P.; Delattre, P. Cyclic changes in the population structure and reproductive pattern of the water vole, *Arvicola terrestris* Linnaeus, 1758. *Mamm. Biol.* **2006**, *71*, 193–202. [CrossRef]
41. Bobretsov, A.V. *The Population Ecology of Small Mammals in Plain and Mountain Landscapes of the North-East of European Russia*; KMK publishers: Moscow, Russia, 2016. (In Russian)
42. Frafjord, K. Population dynamics of an island population of water voles *Arvicola amphibius* (Linnaeus, 1758) with one major predator, the eagle owl *Bubo bubo* (Linnaeus, 1758), in northern Norway. *Polar. Biol.* **2022**, *45*, 1–12. [CrossRef]
43. Formozov, A.N. *An Outline of Ecology of Mouse-Like Rodents—Vectors of Tularemia*; The Moscow Society of Naturalists: Moscow, Russia, 1947. (In Russian)
44. Gromov, I.M.; Erbayeva, M.A. *Mammals of the Fauna of Russia and Adjacent Areas. Lagomorphs and Rodents*; Zoological Institute of the Russian Academy of Sciences: Saint-Petersburg, Russia, 1995. (In Russian)
45. Krasnov, B.R.; Stanko, M.; Morand, S. Host community structure and infestation by ixodid ticks: Repeatability, dilution effect and ecological specialization. *Oecologia* **2007**, *154*, 185–194. [CrossRef]
46. Stanko, M.; Miklisová, D.; de Bellocq, J.G.; Morand, S. Mammal density and patterns of ectoparasite species richness and abundance. *Oecologia* **2002**, *131*, 289–295. [CrossRef]
47. Renwick, A.R.; Lambin, X. Host–parasite interactions in a fragmented landscape. *Int. J. Parasitol.* **2013**, *43*, 27–35. [CrossRef]