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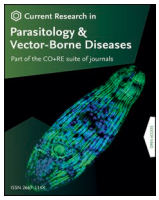

East-to-west dispersal of bird-associated ixodid ticks in the northern Palaearctic: Review of already reported tick species according to longitudinal migratory avian hosts and first evidence on the genetic connectedness of *Ixodes apronophorus* between Siberia and Europe

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ABSTRACT

Birds are long-known as important disseminators of ixodid ticks, in which context mostly their latitudinal, south-to-north migration is considered. However, several bird species that occur in the eastern part of the northern Palaearctic are known to migrate westward. In this study, a female tick collected from the sedge warbler, *Acrocephalus schoenobaenus*, in Lithuania was identified morphologically and analyzed with molecular-phylogenetic methods. In addition, literature data were reviewed on ixodid tick species known to be associated with birds that have recorded east-to-west migratory route in the Palaearctic. The tick collected from *A. schoenobaenus* was morphologically identified as *Ixodes apronophorus*. Two mitochondrial genetic markers for this specimen showed 100% identity with a conspecific tick reported previously in Western Siberia, Russia. Based on literature data, as many as 82 bird species from 11 orders were found to have records of ringing in the easternmost part of the northern Palaearctic and recaptures in Europe. Of these bird species, 31 ixodid tick species were reported in the Euro-Siberian region. Nearly all passeriform bird species with east-to-west migration were reported to carry ticks, whereas no reports of tick infestation were documented from the majority of wetland-associated bird species, mostly from the orders Anseriformes and Charadriiformes. The first European sequences of *bona fide I. apronophorus* revealed genetic connectedness with conspecific ticks reported from Siberia. Since the principal hosts of this tick species are rodents which do not migrate large distances, the most likely explanation for genetic similarity in this direction is dispersal of this tick species *via* migratory birds. Given the high number of tick species that are known to associate with bird species migrating in westward direction, this appears to be an important means of the gene flow between geographically distant tick populations in the northern Palaearctic.

1. Introduction

Birds are long-known as important disseminators of ixodid ticks (Acari: Ixodidae), owing to their short-to-long distance seasonal migration (Hasle et al., 2009). While several ornithophilic tick species frequently feed on birds as adults, usually immature tick developmental stages, larvae and nymphs of other tick species use birds as hosts (Keve et al., 2022). Ixodid tick larvae and nymphs feed on their avian hosts from a few days up to several weeks depending on their three- or two-host life-cycle, respectively (Babos, 1964; Magano et al., 2000).

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During this time long distance migrating passerine birds can fly with a speed of up to 260 km per day (Yohannes et al., 2009), implying a cumulative distance of up to thousands of kilometers during their spring or autumn migration. Although wetland-associated birds are less frequent carriers of ixodid ticks (Pitó et al., 2024), the great snipe (*Gallinago media*) and the bar-tailed godwit (*Limosa lapponica*) are capable of flying over 1000 km per day (Klaassen et al., 2011; Battley et al., 2012). These data imply the possibility of tick translocation by birds over up to thousands of kilometers during spring or autumn migration, confirming the significant role of avian hosts in long distance connectedness between even geographically distant populations of ticks, and even of any associated, tick-borne pathogens.

In this context, mostly latitudinal (south-to-north) migration has been studied, in both Europe (Hasle et al., 2009; Hornok et al., 2022) and Asia (Byun et al., 2024). However, several bird species that occur in the eastern part of the northern Palaearctic are known to migrate westward. For instance, nearly a quarter of indigenous bird species from the Tomsk region of Siberia (Russia) spend their winter in Europe (Korobitsyn et al., 2021). Furthermore, there is an indication of the growing importance of this east-to-west migration in Eurasia owing to climate change and global warming (Dufour et al., 2021).

Previously, genetic evidence has also revealed the consequences of longitudinal (east-to-west) bird migration in Eurasia, in terms of both ticks and tick-borne pathogens. The importance of east-to-west genetic connectedness was recognized in the case of the second most common ixodid tick species associated with avian hosts in Central Europe, i.e. *Haemaphysalis concinna* showing near genetic identity of specimens collected in Europe and the Far East (Hornok et al., 2016). Far Eastern tick-borne *Babesia* genotypes were also shown to be present in Europe (Flaisz et al., 2017), and the same is true for various tick-borne viruses (Subbotina and Loktev, 2012; Ponomareva et al., 2015).

The aim of this review was to collect data of tick species according to their avian hosts that are potentially carried in the east-to-west direction in the northern Palaearctic, most notably between Russia and Europe. The apropos of reviewing relevant literature data was that a female *Ixodes apronophorus* was found on a sedge warbler (*Acrocephalus schoenobaenus*) in Lithuania, which is considered a rare tick species on birds and has not yet been molecularly analyzed in the above context.

2. Materials and methods

2.1. Sample collection and morphological identification of the tick species

The female of *I. apronophorus* that served as the initiative of this study and review was collected from the sedge warbler (*A. schoenobaenus*) on June 15, 2022, in Lithuania. The tick was preserved in 96% ethanol. The specimen was morphologically identified according to standard keys (Filippova, 1977; Rar et al., 2020). Pictures and measurements were made with a VHX-5000 digital microscope (Keyence Co., Osaka, Japan).

2.2. Molecular and phylogenetic analysis

The tick surface was disinfected with 10% sodium-hypochlorite, followed by DNA extraction from one of its legs with the QIAamp DNA Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions, including overnight digestion in tissue lysis buffer and Proteinase K at 56 °C. An extraction control (tissue lysis buffer) was also processed with the tick sample to monitor cross-contamination.

PCR amplification of ~710-bp long fragment of the cytochrome *c* oxidase subunit 1 (*cox*1) gene was performed with the primers LCO1490 (5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′) and HCO2198 (5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′) (Folmer et al., 1994). Another PCR was used to amplify ~460-bp long fragment of the *16S* rDNA gene (Black and Piesman, 1994), with the primers 16S+1 (5′-CTG CTC AAT GAT TTT TTA AAT TGC TGT GG-3′) and 16S-1 (5′-CCG GTC TGA ACT CAG ATC AAG T-3′). PCR reaction mixture components and cycling conditions were the same as reported by Keve et al. (2022). In all PCRs, non-template reaction mixture served as a negative control. The extraction control and negative controls remained PCR-negative in all tests. Purification and sequencing of the PCR amplicons were done by Eurofins Biomi Ltd. (Gödöllő, Hungary). Quality control and trimming of sequences were performed with the BioEdit program. Obtained sequences were compared to GenBank data using the BLASTN program (https://blast.ncbi.nlm.nih.gov). The new sequences were submitted to the GenBank database under the accession numbers PP386617 (*cox*1 gene) and PP386618 (*16S* rRNA gene). Sequences from other studies (retrieved from GenBank) included in the phylogenetic analyses had nearly or exactly 100% coverage with the sequences from this study. Sequence datasets were resampled 1000 times to generate bootstrap values. Phylogenetic analyses were conducted with the neighbor-joining method and p-distance model using the program MEGA version 11.0 (Tamura et al., 2021).

2.3. Collection of literature data

Bird species were included based on records of their migration (recaptures) involving Europe and the northern Palaearctic. Bird ringing data were obtained from https://migrationatlas.org. Consequently, scientific databases were checked for reports on the ixodid tick species collected from each of these bird species, using old and new taxonomy, as well as the common name of the bird species in English, and the Latin name of the ixodid tick species as keywords. The following databases were checked: Library of the Russian Academy of Sciences, Springer Link, Web of Science, Zoological Record, PubMed, Google Scholar, as well as CyberLeninka. Bird species with (i) no data on https://migrationatlas.org as of April 30, 2024, (ii) that arrive rarely or periodically in Europe from the Eastern Palaearctic, and (iii) with no ticks reported from them in Europe, were not considered and are listed in Supplementary Tables S1-S2. Bird species names follow Gill et al. (2024).

3. Results

3.1. Morphological, molecular, and phylogenetic analyses of the bird-associated tick from Lithuania

The tick specimen collected from the sedge warbler was morphologically identified as a female *I. apronophorus*, based on the following characters: elongate, rhombus-shaped scutum with nearly straight lateral carinae (concave in their mid-length), with scattered pores and short hair covering especially in the caudal region; areae porosae flanked by a lateral ridge; on the basis capituli prominent, caudally directed cornuae (dorsally) and auriculae (ventrally); presence of syncoxae on coxae I-II; genital aperture horizontal, surrounded by a circular groove, situated between coxae IV; hypostome long, lanceolate, dental formula 2/2 basally, 3/3 medially and 4/4 or more towards the apex (Fig. 1).

The *cox*1 sequence of this tick showed a 100% (644/644 bp) identity only to one sequence for *I. apronophorus* in GenBank (isolate Om-79/1: MH784873) reported from the Omsk region of Western Siberia, Russia. Similarly, the *16S* rRNA sequence of *I. apronophorus* from Lithuania showed a 100% (412/412 bp) identity to that of the same tick specimen deposited in GenBank from the same region (isolate Om-79/1: MH790193). The phylogenetic analysis of concatenated *cox*1-*16S* sequences confirmed that the tick collected in Europe clustered with Western-Siberian isolates of this species (Fig. 2).

3.2. Review of ixodid ticks from birds with recorded east-to-west migration in the northern Palaearctic

In total, 82 bird species, representing 11 orders, were found to have records of easternmost ringing in the eastern part of the northern

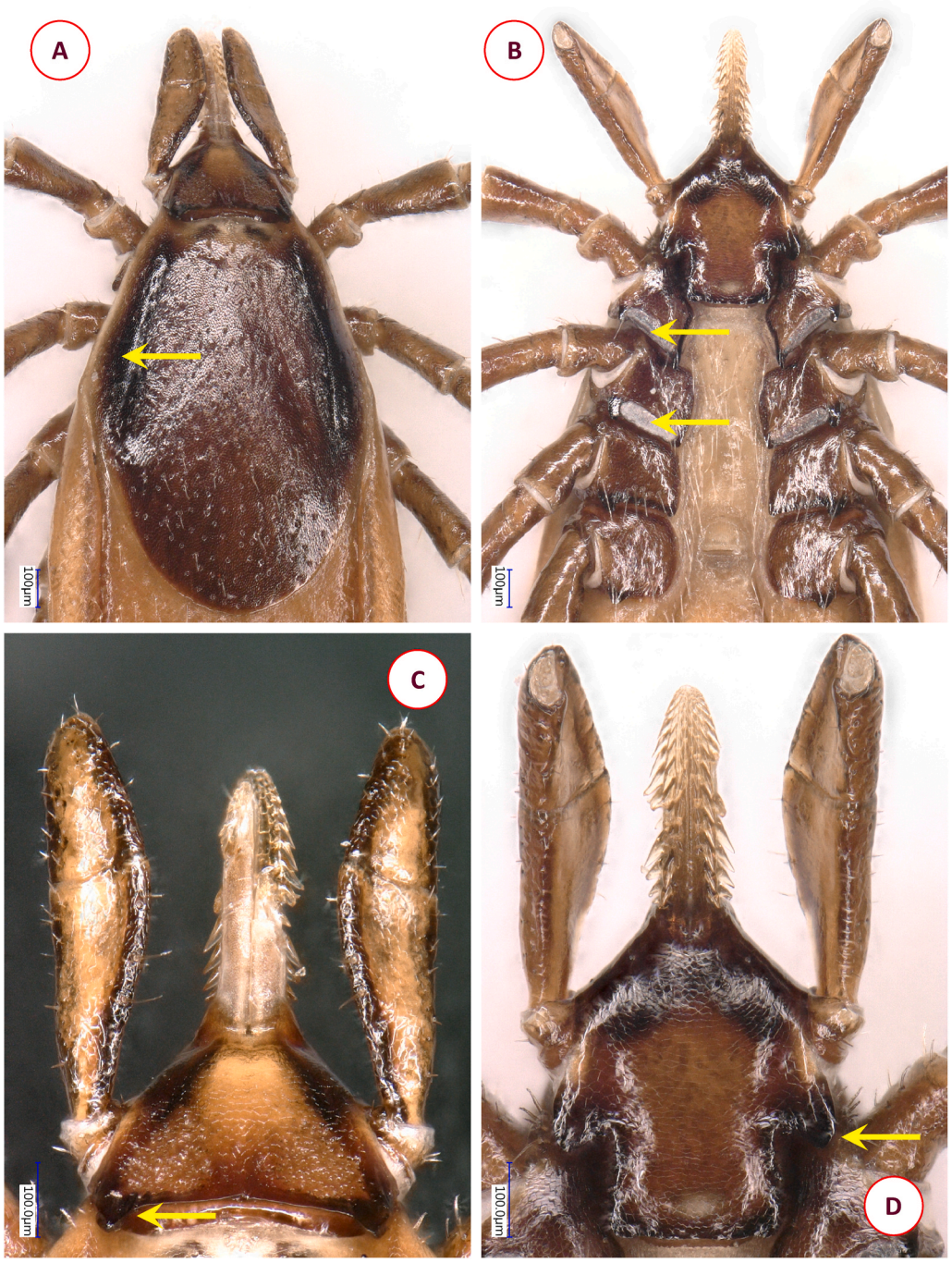

Fig. 1. Morphology of *Ixodes apronophorus*. **A** Dorsal view of scutum, basis capituli and palps (*arrow* indicates the dark area between the scutal margin and nearly straight lateral carinae). **B** Ventral view of coxae, basis capituli and palps (*arrows* mark syncoxae). **C** Dorsal view of basis capituli and palps (*arrow* points at prominent cornua). **D** Ventral view of basis capituli and palps (*arrow* indicates caudally directed, prominent auricula).

Palaearctic and recaptures in Europe (Table 1). Of these bird species, 32 ixodid tick species were reported in the Euro-Siberian region (hereinafter referred to as "East"). The majority of these belonged to the genera *Ixodes* ($n = 15$ in Europe *vs* $n = 7$ in the East) and *Haemaphysalis* ($n = 3$ in Europe *vs* $n = 5$ in the East), while others were represented by a lower number of species: *Hyalomma* ($n = 2$ in Europe *vs* $n = 1$ in the East), *Rhipicephalus* ($n = 1$ in Europe *vs* $n = 3$ in the East) and *Dermacentor* ($n = 1$ in Europe *vs* $n = 2$ in the East). Importantly, eight ixodid tick species (*Ixodes ricinus*, *Ixodes persulcatus*, *Ixodes frontalis*, *Ixodes arboricola*, *Haemaphysalis parva*, *Haemaphysalis punctata*, *Haemaphysalis concinna* and *Hyalomma marginatum*) were reported from the same bird species in both Europe and the Eastern Palaearctic (Table 1). With one exception, nearly all passeriform bird species ($n = 22$) with east-to-west migration were reported to carry ticks, in either the Western or Eastern Palaearctic (Table 1). On the other hand, from 45 bird species with known longitudinal migration in the northern Palaearctic no reports of tick infestation were found, and the great majority of these ($n = 41$) were wetland-associated bird species, mostly of the orders Anseriformes ($n = 21$) and Charadriiformes ($n = 15$) (Supplementary Table S2).

4. Discussion

There are (at least) 91 ixodid tick species indigenous to the Palaearctic realm (Guglielmone et al., 2023). According to literature data

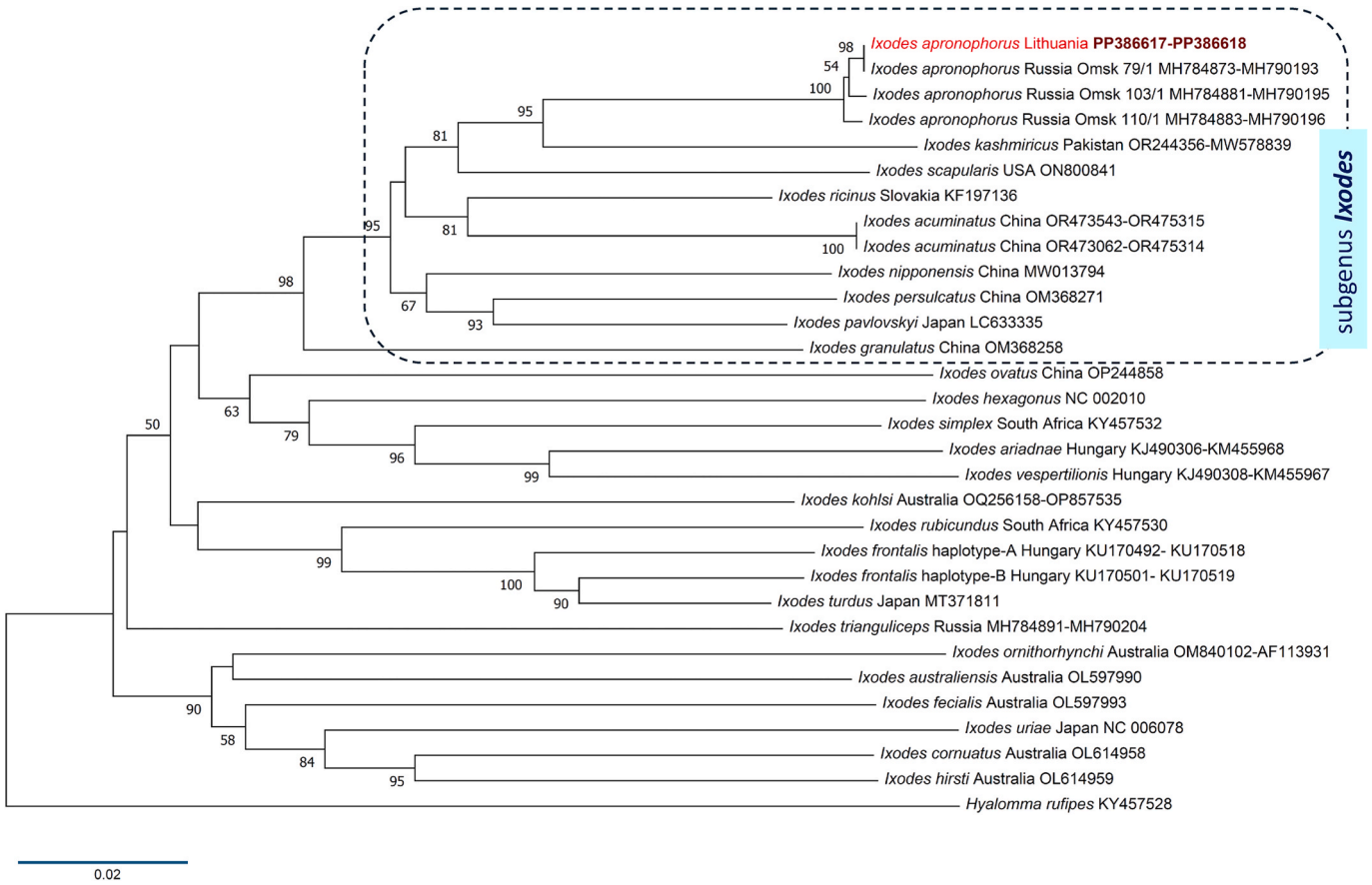

Fig. 2. Phylogenetic tree of *Ixodes* spp. ticks based on concatenated *cox*1 and *16S* gene sequences. *Ixodes apronophorus* collected in this study is marked in red. The evolutionary history was inferred by using the neighbor-joining method based on the p-distance model. The percentage of trees in which the associated taxa clustered together is shown next to the branches. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The analysis involved 31 nucleotide sequences. There were a total of 1059 positions in the final dataset. Evolutionary analyses were conducted in MEGA version 11.0. The sequences for material from China identified as *I. acuminatus* by Liu et al. (2024) probably represent misidentified *Ixodes redikorzevi*. According to Guglielmone et al. (2023) the range of *I. acuminatus* is in the Western Palaearctic (supported by the data in Table 1), whereas that of *I. redikorzevi* is in the Eastern Palaearctic.

reviewed in this paper, a significant ratio of these, i.e. 34% (n = 31 species) can be transported by migratory birds between the eastern and western parts of the northern Palaearctic. This is well reflected by ornithological data, attesting at least 82 bird species with longitudinal migration, i.e. after breeding in Siberia migrating to wintering grounds in Europe. In addition, genetic data also support gene flow and genetic exchange between tick populations in this direction, as outlined below.

In this study, the female of *I. apronophorus* (also called the marsh tick) was collected for the first time from any avian host. This is a relatively rare, nidicolous (endophilic) three-host tick species occurring in northern parts of the temperate zone in Eurasia, where it prefers habitats of moist forests and wetlands, as well as marshes, banks of rivers and water reservoirs, i.e. it is hygrophilous (Filippova, 1977; Guo et al., 2016; Sándor, 2017; Rar et al., 2020; Karimov et al., 2022). Considering the seasonality of *I. apronophorus*, in Russia the larvae and other developmental stages are most abundant on rodents in June (Sukhomlinova, 1977). This also corresponds to the present finding of a female on a sedge warbler in mid-June. This bird species is associated with reedbed habitats, likely to be shared with this hygrophilous tick species.

Taxonomically, *I. apronophorus* belongs to the subgenus *Ixodes*, which contains the highest number of species within the largest monophyletic group of ixodid ticks, the genus *Ixodes* (Filippova, 1977; Rar et al., 2020). At the same time, there is only one report with verified data on the molecular-phylogenetic properties of *I. apronophorus* (Rar et al., 2020), i.e. it is a neglected area of research. Similarly, few studies targeted tick-borne pathogens in this tick species, but recently rickettsiae (Igolkina et al., 2023) and borreliae (Sabitova et al., 2023) have been demonstrated from *I. apronophorus* in Siberia.

The exact geographical range of *I. apronophorus* includes most parts of Europe (except Scandinavia and the Mediterranean region) where it was reported sporadically (Sándor, 2017). Among the Baltic States, most relevant to our finding, *I. apronophorus* was reported from Estonia, Latvia and Lithuania (Kitryté and Baltrunaité, 2023). In Kazakhstan, this species is endemic in the region of Lake Balkas, and in Russia in the Western Siberia (Fedorov and Hornok, 2024) where it shows mosaic-like local occurrence (Rar et al., 2016).

In Europe, *I. apronophorus* was reported from at least 15 rodent species and three species of insectivores (Sándor, 2017). Occasionally, it is also found on medium- to large-sized mammals, such as the wild boar, the red fox and the cat (Sándor, 2017; Kocoń et al., 2022). In Kazakhstan and Russia, *I. apronophorus* was reported from 33 mammalian host species, including rodents (n = 20), insectivores (n = 9), carnivores (n = 3) and lagomorphs (n = 1) (Fedorov and Hornok, 2024). It was also collected form rats in northwestern China (Zhang et al., 2019). In the northern Palaearctic, *I. apronophorus* was reported from nine species of avian hosts in Belarus, Poland, Russia, and Ukraine (Table 2).

In light of the above, in the whole of Eurasia *I. apronophorus* is less often reported from birds than from its typical hosts, rodents (Turcek, 1953; Grebenyuk, 1966; Nosek and Sixl, 1972; Gilot et al., 1976; Zając et al., 2022). To our knowledge, this tick species removed from a sedge warbler in the present study, has never been collected from any bird species in Europe. The merits of this finding are further increased by the first molecular-phylogenetic analysis of *bona fide I. apronophorus* from

Table 1
Ixodid tick species reported in Europe and the northern Palaearctic from bird species with documented migratory routes between the Eastern Palaearctic and Europe. Bird ringing data were obtained from https://migrationatlas.org.

Bird species	Easternmost region of recapture in the Eastern Palaearctic	European origin of the ringed bird	Reported ixodid tick species in the Euro-Siberian region			
			Europe		Eastern Palaearctic	
			Tick species	Reference	Tick species	Reference
Passeriformes						
Acanthis flammea/A. cabaret (syn. *Carduelis flammea/C. cabaret*) (Common/Lesser redpoll)	Eastern China	Northern Europe	*I. ricinus*	Martyn (1988); Comstedt et al. (2006); Wilhelmsson et al. (2020); Keve et al. (2022)		
Bombycilla garrulus (Bohemian waxwing)	Amur Oblast (RF)	Hungary	*I. frontalis*	Krcmar (2012)		
			I. ricinus	Mihalca et al. (2012)		
Carpodacus erythrinus (Common rosefinch)	Kazakhstan, Uzbekistan	Finland, Norway			*I. pavlovskyi* (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
					I. persulcatus (Sverdlovsk Oblast, RF)	Livanova and Livanov (2010)
					I. persulcatus (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
			I. ricinus	Comstedt et al. (2006); Siuda et al. (2006); Paulauskas et al. (2009); Kjelland et al. (2010); Spitalská et al. (2011); Geller et al. (2013); Radzijevskaja et al. (2016)		
Corvus frugilegus (Rook)	Kurgan, Yekaterinburg (former Sverdlovsk) (RF)	Czechia, Germany	*I. arboricola*	Sándor et al. (2017)		
			I. frontalis	Martyn (1988)	*I. frontalis* (Stavropol Krai, Dagestan, RF)	Gusev et al. (1961); Tsapko (2017)
			I. ricinus	Siuda et al. (2006); Nebogatkin (2014); Sándor et al. (2017); Morozov et al. (2022)	*I. ricinus* (Voronezh, RF)	Gaponov and Tewelde (2021)
			Ha. concinna	Sándor et al. (2017)		
			Ha. parva	Sándor et al. (2017)	*Ha. parva* (Ciscaucasia, RF)	Tsapko (2023)
			Ha. punctata	Akimov and Nebogatkin (2012); Sándor et al. (2017)	*Ha. punctate* (Ciscaucasia, Greater Caucasus, RF)	Gusev et al. (1961); Tsapko (2017)
			Hy. marginatum	Akimov and Nebogatkin (2011)	*Hy. marginatum* (Ciscaucasia, Dagestan, RF)	Tsapko (2017)
					R. rossicus (Ciscaucasia, RF)	Tsapko (2023)
					R. sanguineus (Ciscaucasia, RF)	Tsapko (2023)
					R. turanicus (Ciscaucasia, RF)	Tsapko (2023)
Corvus monedula (Eurasian jackdaw)	Perm (RF)	Germany	*I. arboricola*	Martyn (1988); Jaenson et al. (1994); Obsomer et al. (2013); Sándor et al. (2017)		
			I. caledonicus	Martyn (1988)		
			I. ricinus	Ferianc and Lichard (1967); Sándor et al. (2017)	*I. ricinus* (Voronezh, RF)	Gaponov and Tewelde (2021)
					D. marginatus (Ciscaucasia, RF)	Tsapko (2023)
			Ha. parva	Sándor et al. (2017)	*Ha. parva* (Ciscaucasia, RF)	Tsapko (2023)
			Ha. punctata	Martyn (1988); Sándor et al. (2017)	*Ha. punctata* (Ciscaucasia, Greater Caucasus, RF)	Tsapko (2017)
					Ha. sulcata (Ciscaucasia, RF)	Tsapko (2023)
			Hy. marginatum	Sándor et al. (2017)	*Hy. marginatum* (Ciscaucasia, RF)	Kotti et al. (2001)
					R. rossicus (Ciscaucasia, RF)	Tsapko (2023)
Delichon urbicum (Western house martin)	Samara (RF)	Denmark	*I. arboricola*	Nordberg (1936); Fain (1990)		

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Table 1 (*continued*)

Bird species	Easternmost region of recapture in the Eastern Palaearctic	European origin of the ringed bird	Reported ixodid tick species in the Euro-Siberian region			
			Europe		Eastern Palaearctic	
			Tick species	Reference	Tick species	Reference
					I. berlesei (Novosibirsk Oblast, RF)	Yakimenko et al. (2013); Kovalevskiy et al. (2018)
			I. ricinus	Martyn (1988); Papadopoulos et al. (2002)		
			R. cf. *simus*	Aeschlimann and Büttiker (1975)		
Erithacus rubecula (Eurasian robin)	Mongolia	Germany	*I. acuminatus*	Sándor et al. (2014)		
			I. arboricola	Martyn (1988); Jaenson et al. (1994); Hasle et al. (2009); Spitalská et al. (2011); Mihalca et al. (2012); Sándor et al. (2014)		
			I. eldaricus	Nowak-Chmura (2012)		
			I. frontalis	Kaiser et al. (1974); Chastel et al. (1991); Osacar-Jimenez et al. (1998); Papadopoulos et al. (2002); Poupon et al. (2006); Jameson and Medlock (2011); Norte et al. (2012); Nowak-Chmura et al. (2012); Norte et al. (2013); Literak et al. (2015); Norte et al. (2015); Palomar et al. (2015b); Diakou et al. (2016); Hornok et al. (2016); Palomar et al. (2017); Ciebiera et al. (2019); Battisti et al. (2020); Wilhelmsson et al. (2020); Keve et al. (2023); Keve et al. (2024); Pitó et al. (2024)		
			I. persulcatus	Ghibet et al. (1965)	*I. persulcatus* (Novgorod Oblast, RF)	Grigor'eva (2001)
					I. persulcatus (Sverdlovsk Oblast, RF)	Livanova and Livanov (2010)
			I. ricinus	Arthur (1952); Thompson and Arthur (1955); Thompson and Arthur (1956); Brinck et al. (1965); Ferianc and Lichard (1967); Kaiser et al. (1974); Garben et al. (1978); Humair et al. (1993); Jaenson et al. (1994); Hubálek et al. (1996); Osacar-Jimenez et al. (1998); Björsdorff et al. (2001); Papadopoulos et al. (2002); Hanincová et al. (2003); Mannelli et al. (2005); Comstedt et al. (2006); Kipp et al. (2006); Poupon et al. (2006); Spitalská et al. (2006); Humair et al. (2007); Morán Cadenas et al. (2007); Michalik et al. (2008); Movila et al. (2008); Dubska et al. (2009); Hasle et al. (2009); Palomar et al. (2012); Paulauskas et al. (2009); Elfving et al. (2010); Franke et al. (2010a, b); Hildebrandt et al. (2010); Kjelland et al. (2010); Hasle et al. (2011); Hildebrandt et al. (2011); Dubska et al. (2011); James et al. (2011); Spitalská et al. (2011);Žėkienė et al. (2011); Falchi et al. (2012); Marsot et al. (2012); Mihalca et al. (2012); Norte et al. (2012); Nowak-Chmura et al. (2012); Geller et al. (2013); Hornok et al. (2013); Mancini et al. (2013); Norte et al. (2013); Obsomer et al. (2013); Capligina et al. (2014); Hornok et al. (2014); Lommano et al. (2014); Sándor et al. (2014); Kazarina et al. (2015); Palomar et al. (2015b); Berthová et al. (2016); Biernat et al. (2016); Hajduskova et al. (2016); Radzijevskaja et al. (2016); Heylen et al. (2017); Llopis et al. (2017); Pajoro et al. (2018); Ciebiera et al. (2019); Hornok et al. (2019); Klitgaard et al. (2019); Tokarevich et al. (2019); Wilhelmsson et al. (2020); Aleksandrova et al. (2021); Morozov et al. (2022); Keve et al. (2023); Keve et al. (2024); Pitó et al. (2024)	*I. ricinus* (Kaliningrad Oblast, RF)	Movila et al. (2013)
					I. ricinus (Voronezh, RF)	Gaponov et al. (2008)
			I. ventalloi	Rollins et al. (2021)		
			D. reticulatus	Ciebiera et al. (2019)		
			Ha. concinna	Ferianc and Lichard (1967); Hubálek et al. (1996); Hornok et al. (2013); Hornok et al. (2016); Flaisz et al. (2017); Keve et al. (2023)		
			Ha. punctata	Walter and Massa (1987); Martyn (1988); Osacar-Jimenez et al. (1998); Literak et al. (2015); Norte et al. (2015); Aleksandrova et al. (2021)		
			Hy. marginatum	Kaiser et al. (1974); Poupon et al. (2006); Hornok et al. (2013); Vial et al. (2016); Hubálek et al. (2020a,b); Wilhelmsson et al. (2020); Keve et al. (2024)		
			Hy. rufipes	Kaiser et al. (1974); Battisti et al. (2020)		

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Table 1 (*continued*)

Bird species	Easternmost region of recapture in the Eastern Palaearctic	European origin of the ringed bird	Reported ixodid tick species in the Euro-Siberian region			
			Europe		Eastern Palaearctic	
			Tick species	Reference	Tick species	Reference
Ficedula hypoleuca (European pied flycatcher)	Bashkortostan (RF)	France	*I. arboricola*	Martyn (1988); Jaenson et al. (1994); Petney et al. (2012); Van Oosten et al. (2014)		
			I. frontalis	Martyn (1988)		
					I. pavlovskyi (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
					I. persulcatus (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
			I. ricinus	Brinck et al. (1965); Martyn (1988); Björsdorff et al. (2001); Papadopoulos et al. (2002); Nowak-Chmura et al. (2012); Obsomer et al. (2013); Sándor et al. (2014); Norte et al. (2015); Heylen et al. (2017)		
			Hy. marginatum	Palomar et al. (2015b)		
			Hy. rufipes	Pascucci et al. (2019); Keve et al. (2024)		
Fringilla coelebs (Eurasian chaffinch)	Yekaterinburg (former Sverdlovsk, RF)	France	*I. acuminatus*	Mihalca et al. (2012)		
			I. festai	Papadopoulos et al. (2002)		
			I. frontalis	Martyn (1988)		
					I. pavlovskyi (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
			I. persulcatus	Ghibet et al. (1965); Grigoryeva and Markov (2011)	*I. persulcatus* (Novgorod Oblast, RF)	Grigor'eva (2001)
					I. persulcatus (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
			I. ricinus	Brinck et al. (1965); Ferianc and Lichard (1967); Garben et al. (1978); Humair et al. (1993); Hubálek et al. (1996); Osacar-Jimenez et al. (1998); Alekseev et al. (2001); Björsdorff et al. (2001); Papadopoulos et al. (2002); Hanincová et al. (2003); Mannelli et al. (2005); Comstedt et al. (2006); Skotarczak et al. (2006); Spitalská et al. (2006); Humair et al. (2007); Morán Cadenas et al. (2007); Michalik et al. (2008); Movila et al. (2008); Toderas et al. (2008); Hasle et al. (2009); Paulauskas et al. (2009); Franke et al. (2010b); Hildebrandt et al. (2010); Kjelland et al. (2010); Dubska et al. (2011); James et al. (2011); Jameson and Medlock (2011); Movila et al. (2011); Spitalská et al. (2011); Žėkienė et al. (2011); Falchi et al. (2012); Marsot et al. (2012); Mihalca et al. (2012); Norte et al. (2012); Nowak-Chmura et al. (2012); Norte et al. (2013); Obsomer et al. (2013); Lommano et al. (2014); Nebogatkin (2014); Kazarina et al. (2015); Norte et al. (2015); Palomar et al. (2015b); Berthová et al. (2016); Biernat et al. (2016); Radzijevskaja et al. (2016); Heylen et al. (2017); Cull et al. (2018); Pajoro et al. (2018); Ciebiera et al. (2019); Tokarevich et al. (2019); Hornok et al. (2020); Aleksandrova et al. (2021); Keve et al. (2023)	*I. ricinus* (Kaliningrad Oblast, RF) *I. ricinus* (Stavropol Krai, Dagestan, RF)	Movila et al. (2013) Guseva (1962); Tiflova et al. (1970)
			I. ventalloi	Mancuso et al. (2022)		
			Ha. concinna	Ferianc and Lichard (1967)		
			Ha. punctata	Osacar-Jimenez et al. (1998); Literak et al. (2015); Norte et al. (2015); Palomar et al. (2015b); Akimov and Nebogatkin (2012)		
			Hy. margiatum	Kaiser et al. (1974); Palomar et al. (2015b); Wilhelmsson et al. (2020)		
			Hy. rufipes	Kaiser et al. (1974)		
Fringilla montifringilla (Brambling)	Khantia-Mansia (RF)	Germany			*I. pavlovskyi* (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)

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Table 1 (*continued*)

Bird species	Easternmost region of recapture in the Eastern Palaearctic	European origin of the ringed bird	Reported ixodid tick species in the Euro-Siberian region			
			Europe		Eastern Palaearctic	
			Tick species	Reference	Tick species	Reference
					I. persulcatus (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
			I. ricinus	Brinck et al. (1965); Alekseev et al. (2001); Papadopoulos et al. (2002); Elfving et al. (2010); Lommano et al. (2014); Wilhelmsson et al. (2020)	*I. ricinus* (Kaliningrad Oblast, RF)	Movila et al. (2013)
Garrulus glandarius (Eurasian jay)	Orenburg (RF)	Germany	*I. arboricola*	Hornok et al. (2020)		
					I. berlesei (Dagestan, RF)	Zolotarev (1956)
			I. frontalis	Martyn (1988); Doby (1999); Norte et al. (2015); Hornok et al. (2020)	*I. frontalis* (Ciscaucasia, RF)	Ohandjanian (1984); Tsapko and Kotti (2017)
			I. persulcatus	Ghibet et al. (1965)		
			I. ricinus	Ferianc and Lichard (1967); Garben et al. (1978); Humair et al. (1993); Hubálek et al. (1996); Papadopoulos et al. (2002); Siuda et al. (2006); Humair et al. (2007); Morán Cadenas et al. (2007); Movila et al. (2008); James et al. (2011); Marsot et al. (2012); Mihalca et al. (2012); Palomar et al. (2012); Norte et al. (2013); Heylen et al. (2017); Hornok et al. (2020)	*I. ricinus* (Kaliningrad Oblast, Ciscaucasia, Greater Caucasus, RF)	Tiflova et al. (1970); Movila et al. (2013); Tsapko (2017)
					D. marginatus (Ciscaucasia, RF)	Tsapko (2023)
					D. reticulatus (Ciscaucasia, RF)	Tsapko (2023)
					Ha. caucasica (Greater Caucasus, RF)	Tsapko (2023)
			Ha. punctata	Norte et al. (2012, 2013); Hornok et al. (2020)	*Ha. punctata* (Ciscaucasia, RF)	Tsapko (2023)
					Ha. sulcata (Ciscaucasia, RF)	Guseva (1962)
			Hy. marginatum	Norte et al. (2013)	*Hy. marginatum* (Ciscaucasia, RF)	Tsapko (2023)
Loxia curvirostra (Red crossbill)	Chelyabinsk, Perm (RF); Turkmenistan	Germany, Italy, Sweden	*I. caledonicus*	Martyn (1988)		
			I. ricinus	Brinck et al. (1965); Martyn (1988)		
			I. uriae	Martyn (1988)		
Luscinia svecica (Bluethroat)	Kyrgyzstan	Sweden	*I. ricinus*	Arthur (1952); Garben et al. (1978); Jaenson et al. (1994); Papadopoulos et al. (2002); Comstedt et al. (2006); Elfving et al. (2010); Kjelland et al. (2010); Hasle et al. (2011); Radzijevskaja et al. (2016); Heylen et al. (2017); Wilhelmsson et al. (2020); Keve et al. (2023); Pitó et al. (2024)		
			Hy. marginatum	Aeschlimann and Büttiker (1975); Hubálek et al. (2020a,b)		
Nucifraga caryocatactes (Spotted nutcracker)	Krasnoyarsk Krai (RF)	Northern Europe	*I. ricinus*	Siuda et al. (2006); Lommano et al. (2014)		
Oenanthe oenanthe (Northern wheatear)	Yekaterinburg (former Sverdlovsk; RF)	Italy			*I. caledonicus* (Julfa, Nakhichevan, Azerbaijan)	Filippova and Panova (1975)
			I. crenulatus	Morozov et al. (2022)		
			I. ricinus	Thompson and Arthur (1956); Jaenson et al. (1994); Jaenson and Jensen (2007); Paulauskas et al. (2009); Lommano et al. (2014); Radzijevskaja et al. (2016)		
			I. uriae	Martyn (1988)		
			Ha. punctata	Martyn (1988); Wilhelmsson et al. (2020)		
			Hy. marginatum	Martyn (1988); Jameson et al. (2012)		
			Hy. rufipes	Kaiser et al. (1974); Hasle et al. (2009); Pascucci et al. (2019); Battisti et al. (2020); Hubálek et al. (2020a,b); Rollins et al. (2021)		
Parus major (Great tit)	Yekaterinburg (former Sverdlovsk; RF)	Germany	*I. acuminatus*	Mihalca et al. (2012); Sándor et al. (2014)		
			I. arboricola	Arthur and Thompson (1953); Brinck et al. (1965); Ferianc and Lichard (1967); Garben et al. (1978); Siuda and Szymański (1991); Jaenson et al.	*I. arboricola* (Goris, Armenia)	Ohandjanian (1984)

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Table 1 (*continued*)

Bird species	Easternmost region of recapture in the Eastern Palaearctic	European origin of the ringed bird	Reported ixodid tick species in the Euro-Siberian region			
			Europe		Eastern Palaearctic	
			Tick species	Reference	Tick species	Reference
				(1994); Akimov and Nebogatkin (2002); Papadopoulos et al. (2002); Literak et al. (2007); Pietzsch et al. (2008); Heylen and Matthysen (2010); Jameson and Medlock (2011); Spitalská et al. (2011); Mihalca et al. (2012); Norte et al. (2012); Nowak-Chmura et al. (2012); Palomar et al. (2012); Petney et al. (2012); Norte et al. (2013); Heylen et al. (2014); Nebogatkin (2014); Sándor et al. (2014); Van Oosten et al. (2014); Norte et al. (2015); Novakova et al. (2015); Palomar et al. (2015a); Cull et al. (2018); Keve et al. (2024); Pitó et al. (2024)		
			I. canisuga	Martyn (1988)		
			I. frontalis	Ferianc and Lichard (1967); Osacar-Jimenez et al. (1998); Doby (1999); Jameson and Medlock (2011); Norte et al. (2012); Norte et al. (2013); Heylen et al. (2014); Norte et al. (2015); Palomar et al. (2015b); Hornok et al. (2016); Pitó et al. (2024)	*I. frontalis* (Stavropol Krai, Dagestan, RF)	Tsapko (2017)
					I. pavlovskyi (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
			I. persulcatus	Grigoryeva and Markov (2011)	*I. persulcatus* (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
					I. persulcatus (Ussurisky Nature Reserve Primorsky Krai, Far East, RF)	Ivanov (2022)
			I. ricinus	Arthur (1952); Thompson and Arthur (1956); Brinck et al. (1965); Ferianc and Lichard (1967); Garben et al. (1978); Walter and Massa (1987); Siuda and Szymański (1991); Humair et al. (1993); Jaenson et al. (1994); Hubálek et al. (1996); Björsdorff et al. (2001); Akimov and Nebogatkin (2002); Papadopoulos et al. (2002); Hanincová et al. (2003); Mannelli et al. (2005); Comstedt et al. (2006); Kipp et al. (2006); Skotarczak et al. (2006); Spitalská et al. (2006); Gallizzi (2007); Humair et al. (2007); Literak et al. (2007); Morán Cadenas et al. (2007); Michalik et al. (2008); Toderas et al. (2008); Dubska et al. (2009); Paulauskas et al. (2009); Elfving et al. (2010); Franke et al. (2010a, b); Heylen and Matthysen (2010); Hildebrandt et al. (2010); Dubska et al. (2011); Hasle et al. (2011); Hildebrandt et al. (2011); James et al. (2011); Jameson and Medlock (2011); Movila et al. (2011); Spitalská et al. (2011); Žėkienė et al. (2011); Falchi et al. (2012); Marsot et al. (2012); Mihalca et al. (2012); Norte et al. (2012); Nowak-Chmura et al. (2012); Geller et al. (2013); Hornok et al. (2013); Norte et al. (2013); Capligina et al. (2014); Heylen et al. (2014); Hornok et al. (2014); Lommano et al. (2014); Nebogatkin (2014); Sándor et al. (2014); Kazarina et al. (2015); Norte et al. (2015); Berthová et al. (2016); Biernat et al. (2016); Hajduskova et al. (2016); Hornok et al. (2016); Heylen et al. (2017); Llopis et al. (2017); Pajoro et al. (2018); Ciebiera et al. (2019); Klitgaard et al. (2019); Tokarevich et al. (2019); Wilhelmsson et al. (2020); Aleksandrova et al. (2021); Morozov et al. (2022); Keve et al. (2023); Pitó et al. (2024)	*I. ricinus* (Kaliningrad Oblast, RF)	Movila et al. (2013)
					I. ricinus (Voronezh, RF)	Gaponov and Tewelde (2021)
					I. ricinus (Ciscaucasia, Greater Caucasus, RF)	Tsapko (2017)
			Ha. concinna	Ferianc and Lichard (1967); Nebogatkin (2014); Hornok et al. (2016); Flaisz et al. (2017); Pitó et al. (2024)	*Ha. concinna* (Ussurisky Nature Reserve, Primorsky Krai, Far East, RF)	Ivanov (2022)
			Ha. punctata	Osacar-Jimenez et al. (1998); Akimov and Nebogatkin (2012); Norte et al. (2015)		
			Hy. marginatum	Santos-Silva et al. (2006); Palomar et al. (2015b)	*Hy. marginatum* (Ciscaucasia, RF)	Tsapko (2017)

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Bird species	Easternmost region of recapture in the Eastern Palaearctic	European origin of the ringed bird	Reported ixodid tick species in the Euro-Siberian region			
			Europe		Eastern Palaearctic	
			Tick species	Reference	Tick species	Reference
Phoenicurus phoenicurus (Common redstart)	Saratov (RF)	Cyprus	*I. acuminatus*	Mihalca et al. (2012)		
			I. arboricola	Jaenson et al. (1994); Ferianc and Lichard (1967); Mihalca et al. (2012)		
			I. caledonicus	Arthur and Thompson (1953)		
			I. frontalis	Chastel et al. (1991); Jameson et al. (2012)		
					I. pavlovskyi (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
			I. persulcatus	Ghibet et al. (1965)	*I. persulcatus* (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
			I. ricinus	Arthur (1952); Thompson and Arthur (1956); Brinck et al. (1965); Ferianc and Lichard (1967); Garben et al. (1978); Jaenson et al. (1994); Björsdorff et al. (2001); Comstedt et al. (2006); Hasle et al. (2009); Franke et al. (2010b); Hasle et al. (2011); Hildebrandt et al. (2010); Marsot et al. (2012); Nowak-Chmura et al. (2012); Geller et al. (2013); Capligina et al. (2014); Lommano et al. (2014); Kazarina et al. (2015); Radzijevskaja et al. (2016); Heylen et al. (2017); Ciebiera et al. (2019); Klitgaard et al. (2019); Tokarevich et al. (2019); Wilhelmsson et al. (2020)	*I. ricinus* (Kaliningrad Oblast, RF)	Movila et al. (2013)
			Ha. punctata	Arthur (1952); Garben et al. (1978); Jaenson et al. (1994); Siuda et al. (2006)		
			Hy. marginatum	Kaiser et al. (1974); Aeschlimann and Büttiker (1975); Martyn (1988); Poupon et al. (2006); Jameson et al. (2012); Pascucci et al. (2019); Hubálek et al. (2020a, b)	*Hy. marginatum* (Ciscaucasia, RF)	Tsapko (2017)
			Hy. rufipes	Kaiser et al. (1974); Hasle et al. (2009); Pascucci et al. (2019); Battisti et al. (2020); Rollins et al. (2021)		
Pyrrhula pyrrhula (Eurasian bullfinch)	Tyumen (RF)	Finland, Germany	*I. arboricola*	Martyn (1988)		
			I. frontalis	Jameson and Medlock (2011)		
			I. persulcatus	Ghibet et al. (1965)	*I. persulcatus* (Novgorod Oblast, RF)	Grigor'eva (2001)
					I. persulcatus (Sverdlovsk Oblast, RF)	Livanova and Livanov (2010)
			I. ricinus	Brinck et al. (1965); Björsdorff et al. (2001); Papadopoulos et al. (2002); Comstedt et al. (2006); Humair et al. (2007); Spitalská et al. (2006); Kipp et al. (2006); Franke et al. (2010a); James et al. (2011); Ciebiera et al. (2019); Klitgaard et al. (2019)		
Spinus spinus (syn. *Carduelis spinus*) (Eurasian siskin)	Yekaterinburg (former Sverdlovsk, RF)	Germany	*I. arboricola*	Nowak-Chmura et al. (2012)		
			I. ricinus	Arthur and Thompson (1953); Papadopoulos et al. (2002); Comstedt et al. (2006); James et al. (2011); Heylen et al. (2017); Ciebiera et al. (2019)		
Turdus iliacus (Redwing)	Krasnoyarsk Krai (RF)	Poland	*I. acuminatus*	Norte et al. (2015)	*I. persulcatus* (Novgorod Oblast, RF)	Grigor'eva (2001)
					I. persulcatus (Sverdlovsk Oblast, RF)	Livanova and Livanov (2010)
					I. persulcatus (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
			I. frontalis	Martyn (1988); Chastel et al. (1991); Doby (1999); Santos-Silva et al. (2011); Norte et al. (2015); Heylen et al. (2017); Wilhelmsson et al. (2020)	*I. frontalis* (Dagestan, RF)	Tsapko (2017)
					I. pavlovskyi (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)

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Table 1 (*continued*)

Bird species	Easternmost region of recapture in the Eastern Palaearctic	European origin of the ringed bird	Reported ixodid tick species in the Euro-Siberian region			
			Europe		Eastern Palaearctic	
			Tick species	Reference	Tick species	Reference
			I. persulcatus	Ghibet et al. (1965)		
			I. ricinus	Thompson and Arthur (1956); Brinck et al. (1965); Jaenson et al. (1994); Alekseev et al. (2001); Papadopoulos et al. (2002); Comstedt et al. (2006); Humair et al. (2007); Paulauskas et al. (2009); Elfving et al. (2010); Franke et al. (2010b); Hildebrandt et al. (2010); Kjelland et al. (2010); Hasle et al. (2011); Mihalca et al. (2012); Nowak-Chmura et al. (2012); Geller et al. (2013); Hornok et al. (2013); Obsomer et al. (2013); Capligina et al. (2014); Hornok et al. (2014); Lommano et al. (2014); Hornok et al. (2016); Radzijevskaja et al. (2016); Heylen et al. (2017); Pajoro et al. (2018); Ciebiera et al. (2019); Wilhelmsson et al. (2020); Keve et al. (2023)		
			I. ventalloi	Norte et al. (2020)		
Turdus philomelos (Song thrush)	Yekaterinburg (former Sverdlovsk, RF)	Belgium, Hungary	*I. acuminatus*	Kaiser et al. (1974)	*I. ricinus* (Kaliningrad Oblast, RF)	Movila et al. (2013)
					I. ricinus (Voronezh, RF)	Gaponov and Tewelde (2021)
			I. arboricola	Hasle et al. (2009); Sándor et al. (2014)		
			I. festai	Contini et al. (2011); Toma et al. (2014)		
			I. frontalis	Kaiser et al. (1974); Homsher and Sonenshine (1977); Chastel et al. (1991); Osacar-Jimenez et al. (1998); Doby (1999); Papadopoulos et al. (2002); Pietzsch et al. (2008); Jameson and Medlock (2011); Jameson et al. (2012); Palomar et al. (2012); Nowak-Chmura et al. (2012); Norte et al. (2013, 2015); Palomar et al. (2015b); Hornok et al. (2016); Heylen et al. (2017); Palomar et al. (2017); Ciebiera et al. (2019); Wilhelmsson et al. (2020); Morozov et al. (2022); Keve et al. (2023)		
					I. pavlovskyi (Kemerovo, RF)	Kovalevskiy et al. (2018)
			I. persulcatus	Ghibet et al. (1965)	*I. persulcatus* (Novgorod Oblast, RF)	Grigor'eva (2001)
					I. persulcatus (Sverdlovsk Oblast, RF)	Livanova and Livanov (2010)
			I. ricinus	Arthur and Thompson (1953); Thompson and Arthur (1955); Thompson and Arthur (1956); Brinck et al. (1965); Ferianc and Lichard (1967); Kaiser et al. (1974); Humair et al. (1993); Jaenson et al. (1994); Hubálek et al. (1996); Alekseev et al. (2001); Björsdorff et al. (2001); Papadopoulos et al. (2002); Hanincová et al. (2003); Mannelli et al. (2005); Comstedt et al. (2006); Kipp et al. (2006); Skotarczak et al. (2006); Spitalská et al. (2006); Humair et al. (2007); Michalik et al. (2008); Movila et al. (2008); Toderas et al. (2008); Dubska et al. (2009); Hasle et al. (2009); Palomar et al. (2012); Paulauskas et al. (2009); Rusev (2009); Elfving et al. (2010); Franke et al. (2010a, b); Hildebrandt et al. (2010); Kjelland et al. (2010); Dubska et al. (2011); Hasle et al. (2011); James et al. (2011); Movila et al. (2011); Žėkienė et al. (2011); Falchi et al. (2012); Krcmar (2012); Marsot et al. (2012); Mihalca et al. (2012); Nowak-Chmura et al. (2012); Geller et al. (2013); Hornok et al. (2013); Norte et al. (2013); Capligina et al. (2014); Hornok et al. (2014); Lommano et al. (2014); Sándor et al. (2014); Wodecka et al. (2024); Kazarina et al. (2015); Norte et al. (2015); Berthová et al. (2016); Biernat et al. (2016); Radzijevskaja et al. (2016); Heylen et al. (2017); Pajoro et al. (2018); Ciebiera et al. (2019); Hornok et al. (2019); Klitgaard et al. (2019); Tokarevich et al. (2019); Wilhelmsson et al. (2020); Morozov et al. (2022); Keve et al. (2023); Pitó et al. (2024)		
			I. ventalloi	Norte et al. (2020)		

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Table 1 (*continued*)

Bird species	Easternmost region of recapture in the Eastern Palaearctic	European origin of the ringed bird	Reported ixodid tick species in the Euro-Siberian region			
			Europe		Eastern Palaearctic	
			Tick species	Reference	Tick species	Reference
			Ha. concinna	Ferianc and Lichard (1967); Hornok et al. (2016); Flaisz et al. (2017); Keve et al. (2023); Pitó et al. (2024)		
			Ha. punctata	Martyn (1988); Osacar-Jimenez et al. (1998); Movila et al. (2008)		
			Hy. marginatum	Kaiser et al. (1974); Kolodziejek et al. (2014); Keve et al. (2024)		
			Hy. rufipes	Kaiser et al. (1974); Battisti et al. (2020)		
Turdus pilaris (Fieldfare)	Kemerovo Oblast (RF)	Western and Central Europe	*I. acuminatus*	Mihalca et al. (2012)		
			I. frontalis	Doby (1999); Drehmann et al. (2019); Pitó et al. (2024)		
					I. pavlovskyi (Kemerovo, RF)	Kalyagin et al. (2010); Kovalevskiy et al. (2018)
					I. pavlovskyi (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
			I. persulcatus	Ghibet et al. (1965)	*I. persulcatus* (Kemerovo, RF)	Kalyagin et al. (2010); Kovalevskiy et al. (2018)
					I. persulcatus (Novgorod Oblast, RF)	Grigor'eva (2001)
					I. persulcatus (Tomsk, RF)	Mikryukova et al. (2014); Moskvitina et al. (2014)
			I. ricinus	Thompson and Arthur (1955); Brinck et al. (1965); Jaenson et al. (1994); Papadopoulos et al. (2002); Comstedt et al. (2006); Siuda et al. (2006); Humair et al. (2007); Paulauskas et al. (2009); Dubska et al. (2011); Mihalca et al. (2012); Obsomer et al. (2013); Radzijevskaja et al. (2016); Drehmann et al. (2019); Hornok et al. (2020);		
			I. ventalloi	Gilot and Perez (1978)		
Anseriformes						
Anas platyrhynchos (Mallard)	Khantia-Mansia (RF)	Estonia, Sweden	*I. ricinus*	Siuda et al. (2006)		
Gruiformes						
Fulica atra (Eurasian coot)	Samara (RF)	Belgium	*I. ricinus*	Siuda et al. (2006)		
Charadriiformes						
Calidris pugnax (syn. *Philomachus pugnax*) (Ruff)	Yakutia, Khabarovsk (RF)	Denmark, Finland, Germany	*Ha. punctata*	Arthur (1955)		
Larus canus (Common gull)	Komi (RF)	Netherlands	*I. ricinus*	Garben et al. (1978); Jaenson et al. (1994)		
Pluvialis apricaria (European golden plover)	Yakutia (RF)	Netherlands	*I. ricinus*	Douglas and Pearce-Higgins (2019)		
Scolopax rusticola (Eurasian woodcock)	Krasnoyarsk Krai (RF)	France	*I. persulcatus*	Ghibet et al. (1965)		
			I. ricinus	Ferianc and Lichard (1967); Martyn (1988); Ciebiera et al. (2019)		
					D. marginatus (Ciscaucasia, RF)	Lazarenko (2016)
			Ha. concinna	Ferianc and Lichard (1967)		
			Ha. punctata	Ferianc and Lichard (1967)		
					Ha. sulcata (Ciscaucasia, RF)	Guseva (1962)
Sterna hirundo (Common tern)	India, Australia (New South Wales)	Finland, Poland, UK	*Ha. punctata*	Martyn (1988)		
Vanellus vanellus (Northern lapwing)	Irkutsk, Buryatia (RF)	Netherlands	*I. frontalis*	Lamontellerie (1954)		
			I. ricinus	Garben et al. (1978), Martyn (1988); Trilar (2004); Newborn et al. (2009)		
					Hy. marginatum (Ciscaucasia, RF)	Tsapko (2017)

(*continued on next page*)

Table 1 (*continued*)

Bird species	Easternmost region of recapture in the Eastern Palaearctic	European origin of the ringed bird	Reported ixodid tick species in the Euro-Siberian region			
			Europe		Eastern Palaearctic	
			Tick species	Reference	Tick species	Reference
Procellariiformes						
Puffinus puffinus (Manx shearwater)	South Australia	UK	*I. rothschildi*	Martyn (1988)		
Pelecaniformes						
Plegadis falcinellus (Glossy ibis)	Samara (RF)	Hungary	*I. ricinus*	Touati et al. (2015)		
					Hy. marginatum (Ciscaucasia, RF)	Tsapko (2017)
Accipitriformes						
Aquila chrysaetos (Golden eagle)	Bashkortostan (RF)	Finland	*I. frontalis* *I. ricinus* *Ha. punctata*	Oswald (1939) Papadopoulos et al. (2002) Oswald (1939)		
Clanga clanga (syn. *Aquila clanga*) (Greater spotted eagle)	Khantia-Mansia (RF)	Finland			*Ha. punctate* (Ciscaucasia, Greater Caucasus, RF)	Gusev et al. (1961)
Strigiformes						
Asio flammeus (Short-eared owl)	Yekaterinburg (former Sverdlovsk, RF)	Finland, Germany	*I. ventalloi*	Santos-Silva et al. (2006)		
					I. frontalis (Dagestan, RF)	Tsapko (2017)
Asio otus (Long-eared owl)	Tyumen, Yekaterinburg (former Sverdlovsk) (RF)	Finland, Germany, Slovakia	*I. arboricola* *I. frontalis* *I. ricinus* *I. ventalloi* *Ha. punctata*	Monerris et al. (2011) Chastel et al. (1991); Doby (1999); Santos-Silva et al. (2006) Martyn (1988); Papadopoulos et al. (2002); Siuda et al. (2006) Thompson and Arthur (1956) Schulze (1932)		
Piciformes						
Dendrocopos major (Great spotted woodpecker)	Yekaterinburg (former Sverdlovsk, RF)	Finland, Poland	*I. arboricola* *I. frontalis* *I. ricinus* *I. trianguliceps*	Hornok et al. (2020) Tovornik (1991) Ferianc and Lichard (1967); Comstedt et al. (2006); Elfving et al. (2010); Fetisov (2018) Fetisov (2018)		

Abbreviations: *I.*, *Ixodes*; *Ha.*, *Haemaphysalis*; *Hy.*, *Hyalomma*; *D.*, *Dermacentor*; *R.*, *Rhipicephalus*; (RF), Russian Federation.

Table 2
Reported avian hosts of *Ixodes apronophorus* in Eurasia.

Location	Bird host (Latin name)	Bird host (Common name)	Reference
Polesia (either Volyn Oblast of Ukraine or Bryansk Oblast of the RF)	*Anas crecca*	Eurasian teal	Adamovich (1968)
Polesia (either Volyn Oblast of Ukraine or Bryansk Oblast of the RF)	*Gallinula chloropus*	Common moorhen	Adamovich (1968)
Belarus	*Motacilla alba*	White wagtail	Savitsky (1963)
Belarus	*Turdus merula*	Common blackbird	Savitsky (1963)
Poland	*Erithacus rubecula*	Eurasian robin	Zając et al. (2022)
Ukraine (north-west of the Black Sea coast)	*Turdus merula*	Common blackbird	Rusev (2009)
RF (Krasnoyarsk Krai, near the Podkamennaya Tunguska River)	*Tetrastes bonasia*	Hazel grouse	Voltsyt (1997)
RF (Caucasus, Republic of Dagestan)	*Saxicola maurus variegatus*	Siberian stonechat	Aliev et al. (2012)
RF (Caucasus, Republic of Dagestan	*Curruca curruca*	Lesser whitethroat	Aliev et al. (2012)
RF (Caucasus, Republic of Dagestan)	*Lullula arborea*	Woodlark	Aliev et al. (2012)

Abbreviation: RF, Russian Federation.

Europe. In particular, the specimens reported under this species name from Romania (Andersson et al., 2018) were likely misidentified, based on morphological and GenBank data probably representing another species, *I. acuminatus* (Rar et al., 2020). For instance, the ticks published from Romania as *I. apronophorus* did not show the presence of syncoxae, and the corresponding *16S* rRNA gene sequence (GenBank: KY853651) had 99% identity with *I. acuminatus* examined by the authors of this study (Hornok et al., 2022) (GenBank: OM200058).

Considering possible misidentifications of *I. apronophorus* collected from birds in the Eastern Palaearctic, the hosts of this tick species are mentioned as "usually rodents, insectivores and small predatory mammals that inhabit biotopes with increased humidity, rarely birds" (Filippova, 1977). In a later work (see table 2 in Voltsyt, 1997), there is a slight morphological uncertainty about the identity of *I. apronophorus* collected from the hazel grouse (*Tetrastes bonasia*). According to all qualitative and morphometric characteristics, the nymphs fall within the limits of variation indicated for this species (Filippova, 1977), except for the shape of the auriculae. Savitsky (1963) and Aliev et al. (2012) mention cases of parasitism of *I. apronophorus* on bird hosts but they did not provide any description of the collected ticks. Nevertheless, in these sources there is no evidence of misidentification.

According to the results from two mitochondrial genetic markers, the molecular properties of *I. apronophorus* removed from a sedge warbler in Lithuania in this study reflected 100% sequence identity to a conspecific tick collected in Siberia, with which it clustered together with high bootstrap value. This supports the ornithological observations suggesting that there is a direct and indirect bird migration connection between Siberia and Europe (Schally et al., 2022), also relevant to populations of avian ectoparasites (including ticks) in this east-to-west direction.

Based on the present review, wetland-associated birds appear to be less important than passerines in the longitudinal dispersal of ticks in the northern Palaearctic, confirming our previous results focusing on latitudinal bird migration (Pitó et al., 2024). However, among the avian hosts of *I. apronophorus* (Table 2), the Eurasian teal (*Anas crecca*) is known to migrate between Western Siberia and Europe, the latter including the Baltic States (Cerritelli et al., 2023), but the common moorhen (*Gallinula chloropus*) also undergoes migration in the west-to-east direction, from northeastern Europe (Ural region) to the Baltic States (https://migrationatlas.org/). In addition, *I. apronophorus* was reported from passerine birds, such as the common blackbird (*Turdus merula*), the European robin (*Erithacus rubecula*) and the white wagtail (*Motacilla alba*), similarly to the present study (Table 2). The host from which *I. apronophorus* was removed in this study, the sedge warbler (*A. schoenobaenus*) is a reed-water-associated bird species, therefore we speculate that the original avian host arrived in that location carrying a nymph from the east. Several reed-associated bird species (e.g. *Acrocephalus* spp.) are known to migrate with a speed of up to 260 km per day (Yohannes et al., 2009), allowing them to cover even one or two thousand kilometers when the larvae or nymphs of *I. apronophorus* feed on them for 3–8 days (Babos, 1964). We hypothesize that this scenario provides the most plausible explanation for the genetic identity between *I. apronophorus* collected in this study in Lithuania and those reported from Siberia (Rar et al., 2016).

Considering literature data on bird species with longitudinal migration in the northern Palaearctic region in general, most bird-associated tick species were reported from different avian host species in Siberia and in Europe (Table 1). Obviously, however, this scenario does not exclude the possibility that genetic connectedness between populations of a tick species in the Eastern and Western Palaearctic can result from dispersal involving various avian hosts (e.g. implying host switch). Nevertheless, it may be more evident to elucidate the probability of gene flow in this direction if those tick species are considered in the first place which were reported from the same longitudinally migrating bird species in both Europe and Russia (Table 1). For instance, genetic exchange, as reflected by sequence similarities between tick populations in the east-to-west direction, is well demonstrated by the near genetic identity of *Ha. concinna* between Central Europe and the Far East (Hornok et al., 2016). Similarly, populations of *I. persulcatus* and *I. pavlovskyi* in Western Siberia do not show mitochondrial genetic heterogeneity in an east-to-western comparison, probably owing to their short- to long-distance transportation by birds (Livanova et al., 2015, 2016), similarly to what was reported on the lack of remarkable geographical pattern between populations of *I. ricinus* in western Europe along this direction (Noureddine et al., 2011). Last but not least, *I. ricinus*, *I. frontalis* and *Hy. marginatum* are the three tick species collected from migratory birds in the Baltic region of Russia (Movila et al., 2013), probably arriving there from the east or from common wintering grounds shared with birds from the east. In line with this, the *cox*1 sequence of *Hy. marginatum* reported from Russia (GenBank: KU130612) has only a single nucleotide difference from a conspecific sequence reported from Europe, Portugal (GenBank: KU130611) (Sands et al., 2017) which in turn is identical with that from Kazakhstan (GenBank: MN841461) (Yang et al., 2021).

5. Conclusions

The first European sequences of *bona fide I. apronophorus* generated in the present study revealed genetic connectedness with conspecific ticks reported from Siberia. Since the principal hosts of this tick species are rodents which do not migrate large distances, the most likely explanation for genetic similarity in this direction is the dispersal of this tick species *via* longitudinal migratory birds. Given the high number of tick species that are known to associate with bird species migrating in a westward direction (from Siberia to wintering grounds in Europe), this appears to be an important means of the gene flow between geographically distant tick populations in the northern Palaearctic.

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Ethical approval

The license for collecting material from birds was issued by the Aplinkos Apsaugos Agentura (permit no. AS-1250 and AS-1252). The birds were released after ringing.

CRediT authorship contribution statement

Andor Pitó: Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing. **Denis Fedorov:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Vojtěch Brlík:** Investigation, Data curation, Writing – review & editing. **Jenő Kontschán:** Visualization, Data curation, Writing – review & editing. **Gergő Keve:** Conceptualization, Data curation, Writing – review & editing. **Attila D. Sándor:** Conceptualization, Methodology, Writing – review & editing. **Nóra Takács:** Investigation, Writing – review & editing. **Sándor Hornok:** Conceptualization, Methodology, Investigation, Supervision, Writing – original draft, Writing – review & editing, All authors read and approved the final manuscript.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data generated or analyzed during this study are included in this published article and its supplementary files. The newly generated sequences were submitted to the GenBank database under the accession numbers PP386617 (*cox*1 gene) and PP386618 (*16S* rRNA gene).

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Appendix A. Supplementary data

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