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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

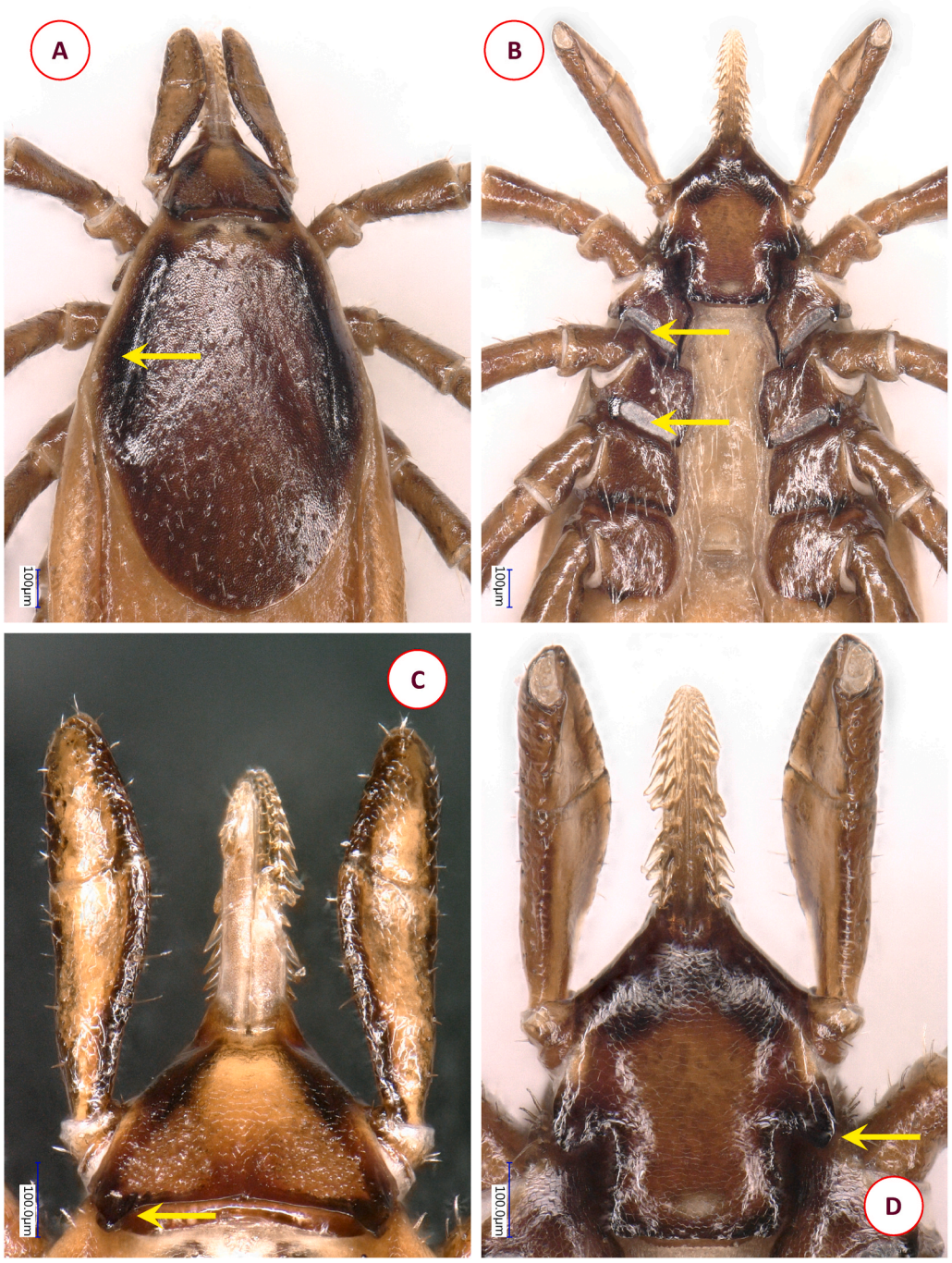


**Fig. 1.** Morphology of *Ixodes apronophorus*. **A** Dorsal view of scutum, basis capituli and palps (*arrow* indicates the dark area between the scutal margin and nearly straight lateral carinae). **B** Ventral view of coxae, basis capituli and palps (*arrows* mark syncoxae). **C** Dorsal view of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

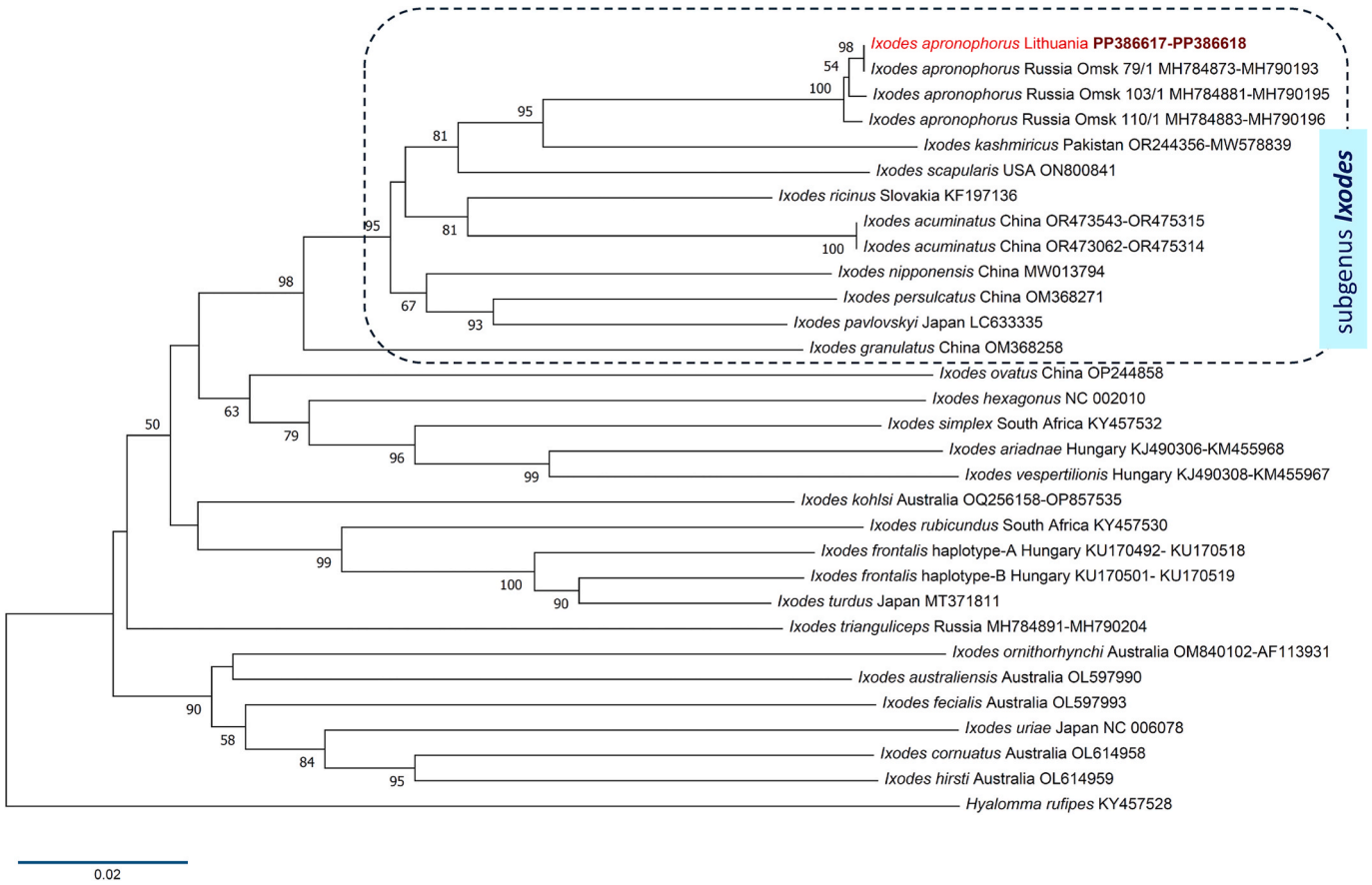


**Fig. 2.** Phylogenetic tree of *Ixodes* spp. ticks based on concatenated *cox*1 and *16S* gene sequences. *Ixodes apronophorus* collected in this study is marked in red. The evolutionary history was inferred by using the neighbor-joining method based on the p-distance model. The percentage of trees 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) | | |

(*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 |
| | | | | | *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)<br>*I. ricinus* (Stavropol Krai, Dagestan, RF) | Movila et al. (2013)<br>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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**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 |
| *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*<br>*I. ricinus*<br>*Ha. punctata* | Oswald (1939)<br>Papadopoulos et al. (2002)<br>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*<br>*I. frontalis*<br>*I. ricinus*<br>*I. ventalloi*<br>*Ha. punctata* | Monerris et al. (2011)<br>Chastel et al. (1991); Doby (1999); Santos-Silva et al. (2006)<br>Martyn (1988); Papadopoulos et al. (2002); Siuda et al. (2006)<br>Thompson and Arthur (1956)<br>Schulze (1932) | | |
| **Piciformes** | | | | | | |
| *Dendrocopos major* (Great spotted woodpecker) | Yekaterinburg (former Sverdlovsk, RF) | Finland, Poland | *I. arboricola*<br>*I. frontalis*<br>*I. ricinus*<br><br>*I. trianguliceps* | Hornok et al. (2020)<br>Tovornik (1991)<br>Ferianc and Lichard (1967); Comstedt et al. (2006); Elfving et al. (2010); Fetisov (2018)<br>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

Supplementary data to this article can be found online at https://doi.org/10.1016/j.crpvbd.2024.100201.

## References

Adamovich, V.L., 1968. [The distribution and phenology of the tick *Ixodes apronophorus* P. Sch. in foci of tularaemia in the Polesie Province]. Parazitologiya 2, 421–423 (In Russian).

Aeschlimann, A., Büttiker, W., 1975. Importations de tiques en Suisse (Acarina: Ixodoidea). Bull. Soc. Entomol. Suisse 48, 69–75.

Akimov, I., Nebogatkin, I., 2002. Ixodid ticks in Kiev. Vestn. Zool. 36, 91–95.

Akimov, I., Nebogatkin, I., 2011. Distribution of the ixodid tick *Hyalomma marginatum* (Ixodoidea, Ixodidae) in Ukraine. Vestn. Zool. 45, 371–374. https://doi.org/10.2478/v10058-011-0022-5.

Akimov, I., Nebogatkin, I., 2012. Distribution of the tick *Haemaphysalis punctata* (Acari, Ixodidae) in Ukraine. Vestn. Zool. 46, 46–51. https://doi.org/10.2478/v10058-012-0030-0.

Aleksandrova, N.I., Christova, I., Dimitrov, D., Marinov, M.P., Panayotova, E., Trifonova, I., et al., 2021. Records of ixodid ticks on wild birds in Bulgaria. Problems Inf. Parasitic Dis. 49, 35–39. https://doi.org/10.58395/pipd.v49i2.65.

Alekseev, A.N., Dubinina, H.V., Semenov, A.V., Bolshakov, C.V., 2001. Evidence of ehrlichiosis agents found in ticks (Acari: Ixodidae) collected from migratory birds. J. Med. Entomol. 38, 471–474. https://doi.org/10.1603/0022-2585-38.4.471.

Aliev, S.K., Mutalimova, R.Z., Alieva, H.S., 2012. [Ixodofauna of passerine birds of Dagestan.] Izvestija Dagestanskogo Gosudarstvennogo Pedagogicheskogo Universiteta. Estestvennye i Tochnye Nauki 4, 14–17 (In Russian).

Andersson, M.O., Radbea, G., Frangoulidis, D., Tomaso, H., Rubel, F., Nava, S., Chitimia-Dobler, L., 2018. New records and host associations of the tick *Ixodes apronophorus* and the first detection of *Ehrlichia* sp. HF in Romania. Parasitol. Res. 117, 1285–1289. https://doi.org/10.1007/s00436-018-5800-3.

Arthur, D.R., 1952. XXXV. Ticks collected from birds in Sweden. Ann. Mag. Nat. Hist. 5, 305–308. https://doi.org/10.1080/00222935208654296.

Arthur, D.R., 1955. Observations on collections of ticks from Denmark. Ent. Medd. 27, 76–81.

Arthur, D.R., Thompson, G.B., 1953. LXXIX. Records of ticks collected from birds in the British Isles. J. Nat. Hist. 6, 797–800. https://doi.org/10.1080/00222935308654485.

Babos, S., 1964. Die Zeckenfauna Mitteleuropas. Akadémiai Kiadó, Budapest.

Battisti, E., Urach, K., Hodžić, A., Fusani, L., Hufnagl, P., Felsberger, G., et al., 2020. Zoonotic pathogens in ticks from migratory birds, Italy. Emerg. Infect. Dis. 26, 2986–2988. https://doi.org/10.3201/eid2612.181686.

Battley, P., Warnock, N., Tibbitts, T., Gill, J.R., Piersma, T., Hassell, C., et al., 2012. Contrasting extreme long-distance migration patterns in bar-tailed godwits *Limosa lapponica*. J. Avi. Biol. 43 https://doi.org/10.1111/j.1600-048X.2011.05473.x.

Berthová, L., Slobodník, V., Slobodník, R., Olekšák, M., Sekeyová, Z., Svitálková, Z., et al., 2016. The natural infection of birds and ticks feeding on birds with *Rickettsia* spp. and *Coxiella burnetii* in Slovakia. Exp. Appl. Acarol. 68, 299–314. https://doi.org/10.1007/s10493-015-9975-3.

Biernat, B., Stańczak, J., Michalik, J., Sikora, B., Cieniuch, S., 2016. *Rickettsia helvetica* and *R. monacensis* infections in immature *Ixodes ricinus* ticks derived from sylvatic passerine birds in west-central Poland. Parasitol. Res. 115, 3469–3477. https://doi.org/10.1007/s00436-016-5110-6.

Björsdorff, A., Bergström, S., Massung, R.F., Haemig, P.D., Olsen, B., 2001. *Ehrlichia*-infected ticks on migrating birds. Emerg. Infect. Dis. 7, 877–879.

Black, W.C., Piesman, J., 1994. Phylogeny of hard- and soft-tick taxa (Acari: Ixodida) based on mitochondrial *16S* rDNA sequences. Proc. Natl. Acad. Sci. USA 91, 10034–10038.

Brinck, P., Svedmyr, A., von Zeipel, G., 1965. Migrating birds at Ottenby Sweden as carriers of ticks and possible transmitters of tick-borne encephalitis virus. Oikos 16, 88–99. https://doi.org/10.2307/3564868.

Byun, H.-R., Rieu, M.-S., Han, S.-W., Ji, S.-R., Nam, H.-Y., Seo, S., 2024. Ixodid ticks from wild and domestic animals in East and Central Asian flyways. Act. Trop. 249, 107091 https://doi.org/10.1016/j.actatropica.2023.107091.

Capligina, V., Salmane, I., Keišs, O., Vilks, K., Japina, K., Baumanis, V., Ranka, R., 2014. Prevalence of tick-borne pathogens in ticks collected from migratory birds in Latvia. Ticks Tick Borne Dis. 5, 75–81. https://doi.org/10.1016/j.ttbdis.2013.08.007.

Cerritelli, G., Vanni, L., Baldaccini, N.E., Lenzoni, A., Sorrenti, M., Giunchi, D., 2023. Trailing the heat: Eurasian teal *Anas crecca* schedule their spring migration basing on the increase in soil temperatures along the route. J. Avian Biol. 2023, e03122 https://doi.org/10.1111/jav.03122.

Chastel, C., Guiguen, C., Chastel, O., Beaucournu, J.C., 1991. Pouvoir pathogène, rôle vecteur et hôtes nouveaux d'*Ixodes pari* (= *I. frontalis*) (Acari; Ixodoidea; Ixodidae). Ann. Parasitol. Hum. Comp. 66, 27–32. https://doi.org/10.1051/parasite/199166127.

Ciebiera, O., Jerzak, L., Nowak-Chmura, M., Bocheński, M., 2019. Ticks (Acari: Ixodida) on birds (Aves) migrating through the Polish Baltic coast. Exp. Appl. Acarol. 77 https://doi.org/10.1007/s10493-019-00341-z.

Comstedt, P., Bergström, S., Olsen, B., Garpmo, U., Marjavaara, L., Mejlon, H., et al., 2006. Migratory passerine birds as reservoirs of Lyme borreliosis in Europe. Emerg. Infect. Dis. 12, 1087–1095. https://doi.org/10.3201/eid1207.060127.

Contini, C., Palmas, C., Seu, V., Stancampiano, L., Usai, F., 2011. Redescription of the male of *Ixodes festai* Rondelli, 1926 (Ixodida: Ixodidae) on specimens from Sardinia (Italy). Parasite 18, 235–240. https://doi.org/10.1051/parasite/2011183235.

Cull, B., Pietzsch, M.E., Hansford, K.M., Gillingham, E.L., Medlock, J.M., 2018. Surveillance of British ticks: An overview of species records, host associations, and new records of *Ixodes ricinus* distribution. Ticks Tick Borne Dis. 9, 605–614. https://doi.org/10.1016/j.ttbdis.2018.01.011.

Diakou, A., Norte, A.C., Lopes de Carvalho, I., Núncio, S., Nováková, M., Kautman, M., et al., 2016. Ticks and tick-borne pathogens in wild birds in Greece. Parasitol. Res. 115, 2011–2016. https://doi.org/10.1007/s00436-016-4943-3.

Doby, J.M., 1999. Contribution to the knowledge of *Ixodes* (*Trichotoixodes*) *pari* Leach (= *I. frontalis* (Panzer)) (Acari: Ixodidae), a tick specific to birds. Acarology 39, 315–325.

Douglas, D., Pearce-Higgins, J., 2019. Variation in ectoparasitic sheep tick *Ixodes ricinus* infestation on European golden plover chicks *Pluvialis apricaria* and implications for growth and survival. Hous. Theor. Soc. 66, 1–11. https://doi.org/10.1080/00063657.2019.1617234.

Drehmann, M., Chitimia-Dobler, L., Lindau, A., Frank, A., Mai, S., Fachet, K., et al., 2019. *Ixodes frontalis*: A neglected but ubiquitous tick species in Germany. Exp. Appl. Acarol. 78, 79–91. https://doi.org/10.1007/s10493-019-00375-3.

Dubska, L., Literak, I., Kocianova, E., Taragelova, V., Sverakova, V., Sychra, O., Hromadko, M., 2011. Synanthropic birds influence the distribution of *Borrelia* species: Analysis of *Ixodes ricinus* ticks feeding on passerine birds. Appl. Environ. Microbiol. 77, 1115–1117. https://doi.org/10.1128/AEM.02278-10.

Dubska, L., Literak, I., Kocianova, E., Taragelova, V., Sychra, O., 2009. Differential role of passerine birds in distribution of *Borrelia* spirochetes, based on data from ticks collected from birds during the post-breeding migration period in Central Europe. Appl. Environ. Microbiol. 75, 596–602. https://doi.org/10.1128/AEM.01674-08.

Dufour, P., de Franceschi, C., Doniol-Valcroze, P., Jiguet, F., Guéguen, M., Renaud, J., Lavergne, S., et al., 2021. A new westward migration route in an Asian passerine bird. Cur. Biol. 31, 5590–5596.e4. https://doi.org/10.1016/j.cub.2021.09.086.

Elfving, K., Olsen, B., Bergström, S., Waldenström, J., Lundkvist, Å., Sjöstedt, A., et al., 2010. Dissemination of spotted fever *Rickettsia* agents in Europe by migrating birds. PLoS One 5, e8572. https://doi.org/10.1371/journal.pone.0008572.

Fain, A., 1990. Les tiques de Belgique (Acari: Ixodoidea). Edition de l'Institut royal des sciences naturelles de Belgique, p. 34.
Falchi, A., Dantas-Torres, F., Lorusso, V., Malia, E., Lia, R., Otranto, D., 2012. Autochthonous and migratory birds as a dispersion source for *Ixodes ricinus* in southern Italy. Exp. Appl. Acarol. 58, 167–174. https://doi.org/10.1007/s10493-012-9571-8.
Fedorov, D., Hornok, S., 2024. Checklist of hosts, illustrated geographical range and ecology of tick species from the genus *Ixodes* (Acari, Ixodidae) in Russia and other post-Soviet countries. ZooKeys 1201, 255–343.
Ferianc, O., Lichard, M., 1967. Birds in the Tribec and Hronský Inovec mountains as hosts of ticks. Bull. World Health Organ. 36 (Suppl. l.), 19–23.
Fetisov, S.A., 2018. About nesting hollows and the evolution of nest building in Picidae woodpeckers: Contacts of woodpeckers with other animals found in their hollows. Russian Ornithol. J. 27, 817–839.
Filippova, N.A., Panova, 1975. Little-known parasite of wild birds, *Ixodes caledonicus* Nuttall, 1910, in the fauna of the USSR (Ixodoidea, Ixodidae)]. Parazitologiya 9, 339–347.
Filippova, N.A., 1977. [Ixodid ticks of the subfamily Ixodinae. Fauna SSSR, 4. Arachnids]. Nauka, Leningrad, p. 178 pp. (In Russian).
Flaisz, B., Sulyok, K.M., Kováts, D., Kontschán, J., Csörgő, T., Csipak, Á., et al., 2017. *Babesia* genotypes in *Haemaphysalis concinna* collected from birds in Hungary reflect phylogeographic connections with Siberia and the Far East. Ticks Tick Borne Dis. 8, 666–670. https://doi.org/10.1016/j.ttbdis.2017.04.013.
Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. Mol. Mar. Biol. Biotechnol. 3, 294–299.
Franke, J., Fritzsch, J., Tomaso, H., Straube, E., Dorn, W., Hildebrandt, A., 2010a. Coexistence of pathogens in host-seeking and feeding ticks within a single natural habitat in Central Germany. Appl. Environ. Microbiol. 76, 6829–6836. https://doi.org/10.1128/AEM.01630-10.
Franke, J., Moldenhauer, A., Hildebrandt, A., Dorn, W., 2010b. Are birds reservoir hosts for *Borrelia afzelii*? Ticks Tick Borne Dis. 1, 109–112. https://doi.org/10.1016/j.ttbdis.2010.03.001.
Gallizzi, K., 2007. Parasite-induced transgenerational effects in the great tit (*Parus major*). PhD Thesis, Universität Bern, Switzerland.
Gaponov, S., Tewelde, R., 2021. Epidemiological survey of birds and their mites in Voronezh. Univ. Proc. Volga Region. Nat. Sci. https://doi.org/10.21685/2307-9150-2021-1-5.
Gaponov, S.P., Fedoruk, S.A., Trankvilevsky, D.V., 2008. Bioecology of ixodid ticks (Ixodidae) in Voronezh. Bull. Voronezh State Univ. Ser. Chemistry, Biology, Pharmacy 2, 71–76.
Garben, A.F.M., Lina, P.H.C., Jansen, J., Van Bronswijk, J., 1978. Teken (Ixodida) van vogels gevangen te Meyendel (Gemeente's-Gravenhage). Entomol. Ber. 38, 156–158.
Geller, J., Nazarova, L., Katargina, O., Leivits, A., Järvekülg, L., Golovljova, I., 2013. Tick-borne pathogens in ticks feeding on migratory passerines in western part of Estonia. Vector Borne Zoonotic Dis. 13, 443–448. https://doi.org/10.1089/vbz.2012.1054.
Ghibet, L.A., Zhmaeva, D.J., Berman, D.J., 1965. [Birds and their importance as a food source of *Ixodes persulcatus* in a natural focus of tick-borne encephalitis in the Kalinin region]. Zool. Zhurnal 44, 228–240.
Gill, F., Donsker, D., Rasmussen, P. (Eds.), 2024. IOC World Bird List, 14.1. https://doi.org/10.14344/IOC.ML.14.1. http://www.worldbirdnames.org/.
Gilot, B., Perez, C., 1978. Individualisation et caracterisation de deux *Ixodes* actuellement confondus: *I. festai* Rondelli, 1926, *I. ventalloi* Gil Collado, 1936 (Acarina, Ixodoidea). Rev. Suisse Zool. 85, 143–149. https://doi.org/10.5962/bhl.part.82224.
Gilot, B., Moncada, E., Pautou, G., 1976. Presence en France d'Ixodes apronophorus (Schulze, 1924). Ixodoidea - Ixodidae. Ann. Parasitol. Hum. Comp. 51, 601-603.
Grebenyuk, R.V., 1966. [Ixodid ticks of Kirghizia]. Academy of Sciences of the Kirghiz SSR, Frunze, 328 pp. (In Russian).
Grigor'eva, L.A., 2001. [Histopathologic changes of bird skin in feeding places of ticks of the genus Ixodes (Acari: Ixodidae)]. Parazitologiya 35, 490–495.
Grigoryeva, L.A., Markov, A.V., 2011. [PCR identification of DNA of hosts of the taiga tick nymphs (*Ixodes persulcatus*: Ixodinae) in St. Petersburg and its suburbs]. Parazitologiya 45, 461–469.
Guglielmone, A.A., Nava, S., Robbins, R.G., 2023. Geographic distribution of the hard ticks (Acari: Ixodida: Ixodidae) of the world by countries and territories. Zootaxa 5251, 1–274. https://doi.org/10.11646/zootaxa.5251.1.1.
Guo, Y., Sun, Y., Xu, R., 2016. The genus *Ixodes* (Acari: Ixodidae) in China with three new record species. Acta Parasitol. 61, 729–742. https://doi.org/10.1515/ap-2016-0102.
Gusev, V.M., Bedny, S.N., Guseva, A.A., Labunets, N.F., Bakeev, N.N., 1961. [Ecological groups of birds of the Caucasus and their role in the life of ticks and fleas]. Trudy Nauchno-Issledovatel'skogo Protivochumnogo Instituta Kavkaza i Zakavkaz'ja 5, 217 (In Russian).
Guseva, A.A., 1962. [To the study of ixodid ticks in Stavropol Krai]. Trudy Azerbaijanskoy Protivochumnoy Stantsii 3, 228–235 (In Russian).
Hajduskova, E., Literak, I., Papousek, I., Costa, F.B., Novakova, M., Labruna, M.B., Zdrazilova-Dubska, L., 2016. "*Candidatus* Rickettsia mendelii", a novel basal group rickettsia detected in *Ixodes ricinus* ticks in the Czech Republic. Ticks Tick Borne Dis. 7, 482–486. https://doi.org/10.1016/j.ttbdis.2016.02.004.
Hanincová, K., Taragelová, V., Koci, J., Schäfer, S.M., Hails, R., Ullmann, A.J., et al., 2003. Association of *Borrelia garinii* and *B. valaisiana* with songbirds in Slovakia. Appl. Environ. Microbiol. 69, 2825–2830. https://doi.org/10.1128/AEM.69.5.2825-2830.2003.
Hasle, G., Bjune, G., Edvardsen, E., Jakobsen, C., Linnehol, B., Røer, J.E., et al., 2009. Transport of ticks by migratory passerine birds to Norway. J. Parasitol. 95, 1342–1351. https://doi.org/10.1645/GE-2146.1.
Hasle, G., Leinaas, H.P., Røed, K.H., Øines, Ø., 2011. Transport of *Babesia venatorum*-infected *Ixodes ricinus* to Norway by northward migrating passerine birds. Acta Vet. Scand. 53, 41. https://doi.org/10.1186/1751-0147-53-41.
Heylen, D., Fonville, M., Docters van Leeuwen, A., Stroo, A., Duisterwinkel, M., van Wieren, S., et al., 2017. Pathogen communities of songbird-derived ticks in Europe's low countries. Parasites Vectors 10, 497. https://doi.org/10.1186/s13071-017-2423-y.
Heylen, D.J.A., Matthysen, E., 2010. Contrasting detachment strategies in two congeneric ticks (Ixodidae) parasitizing the same songbird. Parasitology 137, 661–667. https://doi.org/10.1017/S0031182009991582.
Heylen, D.J.A., Van Oosten, A.R., Devriendt, N., Elst, J., De Bruyn, L., Matthysen, E., 2014. Seasonal feeding activity of the tree-hole tick, *Ixodes arboricola*. Parasitology 141, 1044–1051. https://doi.org/10.1017/S0031182014000225.
Hildebrandt, A., Franke, J., Meier, F., Sachse, S., Dorn, W., Straube, E., 2010. The potential role of migratory birds in transmission cycles of *Babesia* spp., *Anaplasma phagocytophilum*, and *Rickettsia* spp. Ticks Tick Borne Dis. 1, 105–107. https://doi.org/10.1016/j.ttbdis.2009.12.003.
Hildebrandt, A., Fritzsch, J., Franke, J., Sachse, S., Dorn, W., Straube, E., 2011. Co-circulation of emerging tick-borne pathogens in Middle Germany. Vector Borne Zoonotic Dis. 11, 533–537. https://doi.org/10.1089/vbz.2010.0048.
Homsher, P.J., Sonenshine, D.E., 1977. Scanning electron microscopy of ticks for systematic studies. 2. Structure of Haller's organ in *Ixodes brunneus* and *Ixodes frontalis*. J. Med. Entomol. 14, 93–97. https://doi.org/10.1093/jmedent/14.1.93.
Hornok, S., Csorba, A., Kováts, D., Csörgő, T., Hunyadi, A., 2019. Ecdysteroids are present in the blood of wild passerine birds. Sci. Rep. 9, 17002 https://doi.org/10.1038/s41598-019-53090-9.
Hornok, S., Cutajar, B., Takács, N., Galea, N., Attard, D., Coleiro, C., et al., 2022. On the way between Africa and Europe: Molecular taxonomy of ticks collected from birds in Malta. Ticks Tick Borne Dis 13, 102001. https://doi.org/10.1016/j.ttbdis.2022.102001.
Hornok, S., Csörgő, T., de la Fuente, J., Gyuranecz, M., Privigyei, C., Meli, M.L., et al., 2013. Synanthropic birds associated with high prevalence of tick-borne rickettsiae and with the first detection of *Rickettsia aeschlimannii* in Hungary. Vector Borne Zoonotic Dis. 13, 77–83. https://doi.org/10.1089/vbz.2012.1032.
Hornok, S., Flaisz, B., Takács, N., Kontschán, J., Csörgő, T., Csipak, Á., et al., 2016. Bird ticks in Hungary reflect western, southern, eastern flyway connections and two genetic lineages of *Ixodes frontalis* and *Haemaphysalis concinna*. Parasites Vectors 9, 101. https://doi.org/10.1186/s13071-016-1365-0.
Hornok, S., Kováts, D., Csörgő, T., Meli, M.L., Gönczi, E., Hadnagy, Z., et al., 2014. Birds as potential reservoirs of tick-borne pathogens: First evidence of bacteraemia with *Rickettsia helvetica*. Parasites Vectors 7, 128. https://doi.org/10.1186/1756-3305-7-128.
Hornok, S., Kováts, D., Horváth, G., Kontschán, J., Farkas, R., 2020. Checklist of the hard tick (Acari: Ixodidae) fauna of Hungary with emphasis on host-associations and the emergence of *Rhipicephalus sanguineus*. Exp. Appl. Acarol. 80, 311–328. https://doi.org/10.1007/s10493-019-00461-6.
Hubálek, Z., Sedláček, P., Estrada-Peña, A., Vojtíšek, J., Rudolf, I., 2020a. First record of *Hyalomma rufipes* in the Czech Republic, with a review of relevant cases in other parts of Europe. Ticks and Tick-borne Diseases 11, 101421. https://doi.org/10.1016/j.ttbdis.2020.101421.
Hubálek, Z., Anderson, J.F., Halouzka, J., Hájek, V., 1996. Borreliae in immature *Ixodes ricinus* (Acari: Ixodidae) ticks parasitizing birds in the Czech Republic. J. Med. Entomol. 33, 766–771. https://doi.org/10.1093/jmedent/33.5.766.
Hubálek, Z., Sedláček, P., Estrada-Peña, A., Vojtíšek, J., Rudolf, I., 2020b. First record of *Hyalomma rufipes* in the Czech Republic, with a review of relevant cases in other parts of Europe. Ticks Tick Borne Dis 11, 101421. https://doi.org/10.1016/j.ttbdis.2020.101421.
Humair, P.-F., Douet, V., Morán Cadenas, F., Schouls, L.M., Van De Pol, I., Gern, L., 2007. Molecular identification of bloodmeal source in *Ixodes ricinus* ticks using *12S* rDNA as a genetic marker. J. Med. Entomol. 44, 869–880. https://doi.org/10.1603/0022-2585(2007)44[869:miobsi]2.0.co;2.
Humair, P.-F., Turrian, N., Aeschlimann, A., Gern, L., 1993. *Ixodes ricinus* immatures on birds in a focus of Lyme borreliosis. Folia Parasitol. 40, 237–242.
Igolkina, Y., Yakimenko, V., Tikunov, A., Epikhina, T., Tancev, A., Tikunova, N., Rar, V., 2023. Novel genetic lineages of *Rickettsia helvetica* associated with *Ixodes apronophorus* and *Ixodes trianguliceps* ticks. Microorganisms 11, 1215. https://doi.org/10.3390/microorganisms11051215.
Ivanov, A.I., 2022. Summer avifauna of the Suputinsky Nature Reserve. Russian J. Ornithology 31, 3235–3257.
Jaenson, T.G., Tälleklint, L., Lundqvist, L., Olsen, B., Chirico, J., Mejlon, H., 1994. Geographical distribution, host associations, and vector roles of ticks (Acari: Ixodidae, Argasidae) in Sweden. J. Med. Entomol. 31, 240–256. https://doi.org/10.1093/jmedent/31.2.240.
Jaenson, T.G.T., Jensen, J.-K., 2007. Records of ticks (Acari, Ixodidae) from the Faroe Islands. Norw. J. Entomol. 54, 11–15.
James, M.C., Furness, R.W., Bowman, A.S., Forbes, K.J., Gilbert, L., 2011. The importance of passerine birds as tick hosts and in the transmission of *Borrelia burgdorferi*, the agent of Lyme disease: A case study from Scotland. Ibis 153, 293–302. https://doi.org/10.1111/j.1474-919X.2011.01111.x.
Jameson, L.J., Medlock, J.M., 2011. Tick surveillance in Great Britain. Vector Borne Zoonotic Dis. 11, 403–412. https://doi.org/10.1089/vbz.2010.0079.
Jameson, L.J., Morgan, P.J., Medlock, J.M., Watola, G., Vaux, A.G.C., 2012. Importation of *Hyalomma marginatum*, vector of Crimean-Congo haemorrhagic fever virus, into the United Kingdom by migratory birds. Ticks Tick Borne Dis. 3, 95–99. https://doi.org/10.1016/j.ttbdis.2011.12.002.

Kaiser, M.N., Hoogstraal, H., Watson, G.E., 1974. Ticks (Ixodoidea) on migrating birds in Cyprus, fall 1967 and spring 1968, and epidemiological considerations. Bull. Entomol. Res. 64, 97–110. https://doi.org/10.1017/S0007485300027024.

Kalyagin, YuS.K., Zubko, K.S., Efremova, G.V., 2010. [Ixodidae ticks in Kemerovo and the ways of their entry to the city territory: Experience of theoretic research]. Bull. Kemerovo State Univ. 2, 5–10.

Karimov, A.V., Korallo-Vinarskaya, N.P., Kuzmenko, Y.F., Vinarski, M.V., 2022. *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 14, 702. https://doi.org/10.3390/d14090702.

Kazarina, A., Japiņa, K., Keišs, O., Salmane, I., Bandere, D., Capligina, V., Ranka, R., 2015. Detection of tick-borne encephalitis virus in *I. ricinus* ticks collected from autumn migratory birds in Latvia. Ticks Tick Borne Dis. 6, 178–180. https://doi.org/10.1016/j.ttbdis.2014.11.011.

Keve, G., Csörgő, T., Benke, A., Huber, A., Mórocz, A., Németh, Á., et al., 2023. Ornithological and molecular evidence of a reproducing *Hyalomma rufipes* population under continental climate in Europe. Front. Vet. Sci. 10, 1147186 https://doi.org/10.3389/fvets.2023.1147186.

Keve, G., Csörgő, T., Kováts, D., Hornok, S., 2024. Long-term evaluation of factors influencing the association of ixodid ticks with birds in Central Europe, Hungary. Sci. Rep. 14, 4958. https://doi.org/10.1038/s41598-024-55021-9.

Keve, G., Sándor, A.D., Hornok, S., 2022. Hard ticks (Acari: Ixodidae) associated with birds in Europe: Review of literature data. Front. Vet. Sci. 9, 928756 https://doi.org/10.3389/fvets.2022.928756.

Kipp, S., Goedecke, A., Dorn, W., Wilske, B., Fingerle, V., 2006. Role of birds in Thuringia, Germany, in the natural cycle of *Borrelia burgdorferi sensu lato*, the Lyme disease spirochaete. Int. J. Med. Microbiol. 296 (Suppl. 40), 125–128. https://doi.org/10.1016/j.ijmm.2006.01.001.

Kitryté, N., Baltrnaité, L., 2023. Ectoparasitic mites, ticks (Acari: Trombidiformes, Mesostigmata, Ixodida) and insects (Insecta: Psocodea, Siphonaptera) of ground-dwelling small mammals in the Baltic States. An annotated checklist. Zootaxa 5353, 1–46. https://doi.org/10.11646/zootaxa.5353.1.1.

Kjelland, V., Stuen, S., Skarpaas, T., Slettan, A., 2010. *Borrelia burgdorferi sensu lato* in *Ixodes ricinus* ticks collected from migratory birds in southern Norway. Acta Vet. Scand. 52, 59. https://doi.org/10.1186/1751-0147-52-59.

Klaassen, R., Alerstam, T., Carlsson, P., Fox, J., Lindström, Å., 2011. Great flights by great snipes: Long and fast non-stop migration over benign habitats. Biol. Lett. 7, 833–835. https://doi.org/10.1098/rsbl.2011.0343.

Klitgaard, K., Højgaard, J., Isbrand, A., Madsen, J.J., Thorup, K., Bødker, R., 2019. Screening for multiple tick-borne pathogens in *Ixodes ricinus* ticks from birds in Denmark during spring and autumn migration seasons. Ticks Tick Borne Dis. 10, 546–552. https://doi.org/10.1016/j.ttbdis.2019.01.007.

Kocoń, A., Nowak-Chmura, M., Asman, M., 2022. Assessment of the species composition of ticks attacking dogs and domestic cats in the Małopolska and Silesian provinces. Syst. Appl. Acarol. 27, 1509–1517. https://doi.org/10.11158/saa.27.8.3.

Kolodziejek, J., Marinov, M., Kiss, B.J., Alexe, V., Nowotny, N., 2014. The complete sequence of a West Nile virus lineage 2 strain detected in a *Hyalomma marginatum marginatum* tick collected from a song thrush (*Turdus philomelos*) in eastern Romania in 2013 revealed closest genetic relationship to strain Volgograd 2007. PLoS One 9, e109905. https://doi.org/10.1371/journal.pone.0109905.

Korobitsyn, I.G., Moskvitina, N.S., Tyutenkov, O.Y., Gashkov, S.I., Kononova, Y.V., Moskvitin, S.S., et al., 2021. Detection of tick-borne pathogens in wild birds and their ticks in Western Siberia and high level of their mismatch. Folia Parasitol. 68, 24. https://doi.org/10.14411/fp.2021.024.

Kotti, B.K., Shaposhnikova, L.I., Evchenko, I.M., Levchenko, B.I., Surkhaev, D.B., Korzhov, P.N., Tokhov, I.M., 2001. [*Hyalomma marginatum* Koch in Stavropol' region]. Zh. Mikrobiol. Epidemiol. Immunobiol. 6 (Suppl. l.), 105–108.

Kovalevskiy, A.V., Zubko, K.S., Efimova, A.R., Luchnikova, E.M., Drozdova, O.M., 2018. Distribution and some biological features of ixodid ticks (Parasitiformes, Ixodidae) in Kuznetsk-Salair mountain area (Kemerovo Province, Russia). Entomol. Rev. 98, 1379–1388. https://doi.org/10.1134/S0013873818090154.

Krcmar, S., 2012. Hard ticks (Acari, Ixodidae) of Croatia. ZooKeys 234, 19–57. https://doi.org/10.3897/zookeys.234.3658.

Lamontellerie, M., 1954. *Ixodes sigalasi* n. sp., Ixodoide nouveau des oiseaux. Ann. Parasitol. Hum. Comp. 29, 561–567.

Lazarenko, E.V., 2016. Host-parasite relation ticks of the genus *Dermacentor* Koch under Ciscaucasia. Innovation Sci. 3, 28–31.

Literak, I., Kocianová, E., Dusbabek, F., Martinu, J., Podzemny, P., Sychra, O., 2007. Winter infestation of wild birds by ticks and chiggers (Acari: Ixodidae, Trombiculidae) in the Czech Republic. Parasitol. Res. 101, 1709–1711. https://doi.org/10.1007/s00436-007-0702-9.

Literak, I., Norte, A.C., Núncio, M.S., de Carvalho, I.L., Ogrzewalska, M., Nováková, M., et al., 2015. Ticks on passerines from the Archipelago of the Azores as hosts of borreliae and rickettsiae. Ticks Tick Borne Dis. 6, 607–610. https://doi.org/10.1016/j.ttbdis.2015.05.003.

Liu, G., Tan, W., Wang, H., Han, X., Hornok, S., Zhao, S., et al., 2024. The great gerbil (*Rhombomys opimus*) as a host for tick species in Gurbantunggut Desert. Parasites Vectors 17, 55. https://doi.org/10.1186/s13071-024-06160-5.

Livanova, N.N., Livanov, S.G., 2010. Zoological prerequisites of human tick-borne infections in the Northern Urals. Biol. Bull. 37, 741–747. https://doi.org/10.1134/S1062359010070101.

Livanova, N.N., Livanov, S.G., Tikunov, A.Yu, Fomenko, N.V., Tikunova, N.V., 2016. Ecological and molecular genetic features of *Ixodes persulcatus* and *I. pavlovskyi* ticks in Southern West Siberia. Contemp. Probl. Ecol. 9, 730–738. https://doi.org/10.1134/S1995425516060081.

Livanova, N.N., Tikunov, A.Yu, Kurilshikov, A.M., Livanov, S.G., Fomenko, N.V., Taranenko, D.E., et al., 2015. Genetic diversity of *Ixodes pavlovskyi* and *I. persulcatus* (Acari: Ixodidae) from the sympatric zone in the south of Western Siberia and Kazakhstan. Exp. Appl. Acarol. 67, 441–456. https://doi.org/10.1007/s10493-015-9947-7.

Llopis, I.V., Tomassone, L., Grego, E., Silvano, F., Rossi, L., 2017. Investigation into Usutu and West Nile viruses in ticks from wild birds in northwestern Italy, 2012-2014. New Microbiol. 40, 56–57.

Lommano, E., Dvořák, C., Vallotton, L., Jenni, L., Gern, L., 2014. Tick-borne pathogens in ticks collected from breeding and migratory birds in Switzerland. Ticks Tick Borne Dis. 5, 871–882. https://doi.org/10.1016/j.ttbdis.2014.07.001.

Magano, S.R., Els, D.A., Chown, S.L., 2000. Feeding patterns of immature stages of *Hyalomma truncatum* and *Hyalomma marginatum rufipes* on different hosts. Exp. Appl. Acarol. 24, 301–313. https://doi.org/10.1023/A:1006457325097.

Mancini, F., Toma, L., Ciervo, A., Di Luca, M., Faggioni, G., Lista, F., Rezza, G., 2013. Virus investigation in ticks from migratory birds in Italy. New Microbiol. 36, 433–434.

Mancuso, E., Toma, L., Pascucci, I., d'Alessio, S.G., Marini, V., Quaglia, M., Monaco, F., 2022. Direct and indirect role of migratory birds in spreading CCHFV and WNV: A multidisciplinary study on three stop-over islands in Italy. Pathogens 11, 1056.

Mannelli, A., Nebbia, P., Tramuta, C., Grego, E., Tomassone, L., Ainardi, R., et al., 2005. *Borrelia burgdorferi sensu lato* infection in larval *Ixodes ricinus* (Acari: Ixodidae) feeding on blackbirds in northwestern Italy. J. Med. Entomol. 42, 168–175. https://doi.org/10.1093/jmedent/42.2.168.

Marsot, M., Henry, P.-Y., Vourc'h, G., Gasqui, P., Ferquel, E., Laignel, J., et al., 2012. Which forest bird species are the main hosts of the tick, *Ixodes ricinus*, the vector of *Borrelia burgdorferi sensu lato*, during the breeding season? Int. J. Parasitol. 42, 781–788. https://doi.org/10.1016/j.ijpara.2012.05.010.

Martyn, K.P., 1988. Provisional atlas of the ticks (Ixodoidea) of the British Isles. Biological Records Centre. Natural Environment Research Council, London, UK.

Michalik, J., Wodecka, B., Skoracki, M., Sikora, B., Stańczak, J., 2008. Prevalence of avian-associated *Borrelia burgdorferi s.l.* genospecies in *Ixodes ricinus* ticks collected from blackbirds (*Turdus merula*) and song thrushes (*T. philomelos*). Int. J. Med. Microbiol. 298, 129–138. https://doi.org/10.1016/j.ijmm.2008.03.004.

Mihalca, A.D., Dumitrache, M.O., Magdaş, C., Gherman, C.M., Domşa, C., Mircean, V., et al., 2012. Synopsis of the hard ticks (Acari: Ixodidae) of Romania with update on host associations and geographical distribution. Exp. Appl. Acarol. 58, 183–206. https://doi.org/10.1007/s10493-012-9566-5.

Mikryukova, T.P., Moskvitina, N.S., Kononova, Y.V., Korobitsyn, I.G., Kartashov, M.Y., Tyuten'kov, O.Y., et al., 2014. Surveillance of tick-borne encephalitis virus in wild birds and ticks in Tomsk city and its suburbs (Western Siberia). Ticks Tick Borne Dis. 5, 145–151. https://doi.org/10.1016/j.ttbdis.2013.10.004.

Monerris, M., Esquivel, C.C.P., Chueca, M.Á.M., 2011. New records of tick fauna from the Balearic islands (Spain) (Acari: Ixodidae). Bol. Asoc. Española Entomol. 35, 477–481.

Morán Cadenas, F., Rais, O., Humair, P.-F., Douet, V., Moret, J., Gern, L., 2007. Identification of host bloodmeal source and *Borrelia burgdorferi sensu lato* in field-collected *Ixodes ricinus* ticks in Chaumont (Switzerland). J. Med. Entomol. 44, 1109–1117. https://doi.org/10.1603/0022-2585(2007)44[1109:iohbsa]2.0.co;2.

Morozov, A., Tischenkov, A., Silaghi, C., Proka, A., Toderas, I., Movila, A., et al., 2022. Prevalence of bacterial and protozoan pathogens in ticks collected from birds in the Republic of Moldova. Microorganisms 10, 1111. https://doi.org/10.3390/microorganisms10061111.

Moskvitina, N.S., Korobitsyn, I.G., Tyuten'kov, O.Yu, Gashkov, S.I., Kononova, YuV., Moskvitin, S.S., et al., 2014. The role of birds in the maintenance of tick-borne infections in the Tomsk anthropurgic foci. Biol. Bull. 41, 387–393. https://doi.org/10.1134/S1062359014040086.

Movila, A., Alekseev, A.N., Dubinina, H.V., Toderas, I., 2013. Detection of tick-borne pathogens in ticks from migratory birds in the Baltic region of Russia. Med. Vet. Entomol. 27, 113–117. https://doi.org/10.1111/j.1365-2915.2012.01037.x.

Movila, A., Gatewood, A., Toderas, I., Duca, M., Papero, M., Uspenskaia, I., 2008. Prevalence of *Borrelia burgdorferi sensu lato* in *Ixodes ricinus* and *I. lividus* ticks collected from wild birds in the Republic of Moldova. Int. J. Med. Microbiol. 298, 149–153. https://doi.org/10.1016/j.ijmm.2007.12.009.

Movila, A., Reye, A.L., Dubinina, H.V., Tolstenkov, O.O., Toderas, I., Hübschen, J.M., et al., 2011. Detection of *Babesia* sp. EU1 and members of spotted fever group rickettsiae in ticks collected from migratory birds at Curonian Spit, north-western Russia. Vector Borne Zoonotic Dis. 11, 89–91. https://doi.org/10.1089/vbz.2010.0043.

Nebogatkin, I., 2014. Birds as the feeders of ticks (Acari, Ixodida) in megalopolis of Kyiv. Vestn. Zool. 48, 467–470. https://doi.org/10.2478/vzoo-2014-0055.

Newborn, D., Fletcher, K.L., Beeston, R., Baines, D., 2009. Occurrence of sheep ticks on moorland wader chicks. Hous. Theor. Soc. 56, 401–404.

Nordberg, S., 1936. Biologisch-ökologische Untersuchungen über die Vogelnidicolen. Acta Zool. Fenn. 21, 3–168.

Norte, A.C., Margos, G., Becker, N.S., Albino Ramos, J., Núncio, M.S., Fingerle, V., et al., 2020. Host dispersal shapes the population structure of a tick-borne bacterial pathogen. Mol. Ecol. 29, 485–501. https://doi.org/10.1111/mec.15336.

Norte, A.C., da Silva, L.P., Tenreiro, P.J.Q., Felgueiras, M.S., Araújo, P.M., Lopes, P.B., et al., 2015. Patterns of tick infestation and their *Borrelia burgdorferi s.l.* infection in wild birds in Portugal. Ticks Tick Borne Dis. 6, 743–750. https://doi.org/10.1016/j.ttbdis.2015.06.010.

Norte, A.C., de Carvalho, I.L., Ramos, J.A., Gonçalves, M., Gern, L., Núncio, M.S., 2012. Diversity and seasonal patterns of ticks parasitizing wild birds in western Portugal. Exp. Appl. Acarol. 58, 327–339. https://doi.org/10.1007/s10493-012-9583-4.

Norte, A.C., Ramos, J.A., Gern, L., Núncio, M.S., Lopes de Carvalho, I., 2013. Birds as reservoirs for *Borrelia burgdorferi s.l.* in western Europe: Circulation of *B. turdi* and other genospecies in bird-tick cycles in Portugal. Environ. Microbiol. 15, 386–397. https://doi.org/10.1111/j.1462-2920.2012.02834.x.

Nosek, J., Sixl, W., 1972. Central-European ticks (Ixodoidea): Key for determination. Mitt. Abt. Zool. Landesmus. Joanneum. 1, 61–92.

Noureddine, R., Chauvin, A., Plantard, O., 2011. Lack of genetic structure among Eurasian populations of the tick *Ixodes ricinus* contrasts with marked divergence from north-African populations. Int. J. Parasitol. 41, 183–192. https://doi.org/10.1016/j.ijpara.2010.08.010.

Novakova, M., Bulkova, A., Costa, F.B., Kristin, A., Krist, M., Krause, F., et al., 2015. Molecular characterization of "*Candidatus* Rickettsia vini" in *Ixodes arboricola* from the Czech Republic and Slovakia. Ticks Tick Borne Dis. 6, 330–333. https://doi.org/10.1016/j.ttbdis.2015.02.006.

Nowak-Chmura, M., 2012. *Ixodes eldaricus* Djaparidze, 1950 (Ixodidae) on migrating birds reported first time in Poland. Vet. Parasitol. 186, 399–402. https://doi.org/10.1016/j.vetpar.2011.11.029.

Nowak-Chmura, M., Siuda, K., Wegner, Z., Piksa, K., 2012. Species diversity of ticks (Acari: Ixodida) on migrating birds on the Baltic Sea coast of Poland. Zool. Stud. 51, 1411–1417.

Obsomer, V., Wirtgen, M., Linden, A., Claerebout, E., Heyman, P., Heylen, D., et al., 2013. Spatial disaggregation of tick occurrence and ecology at a local scale as a preliminary step for spatial surveillance of tick-borne diseases: General framework and health implications in Belgium. Parasites Vectors 6, 190. https://doi.org/10.1186/1756-3305-6-190.

Ohandjanian, A.M., 1984. [Species of ixodids (Ixodidae) new for the fauna of Armenia]. Parazitologiya 18, 181–182 (In Russian).

Osacar-Jimenez, J.J., Estrada-Peña, A., Lucientes-Curdi, J., 1998. Ticks (Acarina: Ixodidae) of wild birds in the Ebro Middle Basin (north-east Spain). Acarologia 39, 23–31.

Oswald, B., 1939. On Yugoslavian (Balkan) ticks [Ixodoidea]. Parasitology 31, 271–280.

Pajoro, M., Pistone, D., Varotto Boccazzi, I., Mereghetti, V., Bandi, C., Fabbi, M., et al., 2018. Molecular screening for bacterial pathogens in ticks (*Ixodes ricinus*) collected on migratory birds captured in northern Italy. Folia Parasitol. 65, 8. https://doi.org/10.14411/fp.2018.008.

Palomar, A.M., Portillo, A., Crespo, A., Santibáñez, S., Mazuelas, D., Oteo, J.A., 2015a. Prevalence of "*Candidatus* Rickettsia vini" in *Ixodes arboricola* ticks in the north of Spain, 2011–2013. Parasites Vectors 8, 110. https://doi.org/10.1186/s13071-015-0724-6.

Palomar, A.M., Portillo, A., Santibáñez, P., Mazuelas, D., Roncero, L., García-Álvarez, L., et al., 2015b. Detection of tick-borne *Anaplasma bovis, Anaplasma phagocytophilum* and *Anaplasma centrale* in Spain. Med. Vet. Entomol. 29, 349–353. https://doi.org/10.1111/mve.12124.

Palomar, A.M., Portillo, A., Santibáñez, P., Mazuelas, D., Roncero, L., Gutiérrez, Ó., Oteo, J.A., 2017. Presence of *Borrelia turdi* and *Borrelia valaisiana* (Spirochaetales: Spirochaetaceae) in ticks removed from birds in the north of Spain, 2009–2011. J. Med. Entomol. 54, 243–246. https://doi.org/10.1093/jme/tjw158.

Palomar, A.M., Santibáñez, P., Mazuelas, D., Roncero, L., Santibáñez, S., Portillo, A., Oteo, J.A., 2012. Role of birds in dispersal of etiologic agents of tick-borne zoonoses, Spain, 2009. Emerg. Infect. Dis. 18, 1188–1191. https://doi.org/10.3201/eid1807.111777.

Papadopoulos, B., Humair, P.F., Aeschlimann, A., Vaucher, C., Büttiker, W., 2002. Ticks on birds in Switzerland. Acarology 42, 3–19.

Pascucci, I., Di Domenico, M., Capobianco Dondona, G., Di Gennaro, A., Polci, A., Capobianco Dondona, A., et al., 2019. Assessing the role of migratory birds in the introduction of ticks and tick-borne pathogens from African countries: An Italian experience. Ticks Tick Borne Dis. 10, 101272 https://doi.org/10.1016/j.ttbdis.2019.101272.

Paulauskas, A., Rosef, O., Galdikaite, E., Radzijevskaja, J., 2009. Infestation with *Ixodes ricinus* ticks on migrating passerine birds in Lithuania and Norway. Acta Biol. Univ. Daugavpiliensis 9, 1–6.

Petney, T., Pfäffle, M., Skuballa, J., 2012. An annotated checklist of the ticks (Acari: Ixodida) of Germany. Syst. Appl. Acarol. 17, 115–170. https://doi.org/10.11158/saa.17.2.2.

Pietzsch, M.E., Mitchell, R., Jameson, L.J., Morgan, C., Medlock, J.M., Collins, D., et al., 2008. Preliminary evaluation of exotic tick species and exotic pathogens imported on migratory birds into the British Isles. Vet. Parasitol. 155, 328–332. https://doi.org/10.1016/j.vetpar.2008.05.006.

Pitó, A., Bukor, B., Győrig, E., Brlík, V., Kontschán, J., Keve, G., et al., 2024. Investigations of the tick burden on passeriform, water-associated and predatory birds reveal new tick-host associations and habitat-related factors of tick infestation. Parasites Vectors 17, 144. https://doi.org/10.1186/s13071-024-06229-1.

Ponomareva, E.P., Mikryukova, T.P., Gori, A.V., Kartashov, M.Y., Protopopova, E.V., Chausov, E.V., et al., 2015. Detection of Far-Eastern subtype of tick-borne encephalitis viral RNA in ticks collected in the Republic of Moldova. J. Vector Borne Dis. 52, 334–336.

Poupon, M.-A., Lommano, E., Humair, P.-F., Douet, V., Rais, O., Schaad, M., et al., 2006. Prevalence of *Borrelia burgdorferi sensu lato* in ticks collected from migratory birds in Switzerland. Appl. Environ. Microbiol. 72, 976–979. https://doi.org/10.1128/AEM.72.1.976-979.2006.

Radzijevskaja, J., Rosef, O., Matulaityte, V., Paulauskas, A., 2016. *Borrelia burgdorferi sensu lato* genospecies in *Ixodes ricinus* ticks feeding on passerine birds in southern Norway. Biologija 62, 2. https://doi.org/10.6001/biologija.v62i2.3338.

Rar, V., Yakimenko, V., Makenov, M., Tikunov, A., Epikhina, T., Tancev, A., et al., 2016. High prevalence of *Babesia microti* 'Munich' type in small mammals from an *Ixodes persulcatus/Ixodes trianguliceps* sympatric area in the Omsk region, Russia. Parasitol. Res. 115, 3619–3629. https://doi.org/10.1007/s00436-016-5128-9.

Rar, V., Yakimenko, V., Tikunov, A., Vinarskaya, N., Tancev, A., Babkin, I., et al., 2020. Genetic and morphological characterization of *Ixodes apronophorus* from western Siberia, Russia. Ticks Tick Borne Dis. 11, 101284 https://doi.org/10.1016/j.ttbdis.2019.101284.

Rollins, R.E., Schaper, S., Kahlhofer, C., Frangoulidis, D., Strauß, A.F.T., Cardinale, M., et al., 2021. Ticks (Acari: Ixodidae) on birds migrating to the island of Ponza, Italy, and the tick-borne pathogens they carry. Ticks Tick Borne Dis. 12, 101590 https://doi.org/10.1016/j.ttbdis.2020.101590.

Rusev, I.T., 2009. [Species structure, number and biotope distribution of ticks in the north-western coast of the Black Sea]. Visnik Odes'kogo Nacional'nogo Universitetu. Biologiya 14, 89–101. https://doi.org/10.18524/2077-1746.2009.14.181928 (In Russian).

Sabitova, Y., Rar, V., Tikunov, A., Yakimenko, V., Korallo-Vinarskaya, N., Livanova, N., Tikunova, N., 2023. Detection and genetic characterization of a putative novel *Borrelia* genospecies in *Ixodes apronophorus/Ixodes persulcatus/Ixodes trianguliceps* sympatric areas in Western Siberia. Ticks Tick Borne Dis. 14, 102075 https://doi.org/10.1016/j.ttbdis.2022.102075.

Sándor, A.D., 2017. *Ixodes apronophorus* Schulze, 1924. In: Estrada-Peña, A., Mihalca, A., Petney, T. (Eds.), Ticks of Europe and North Africa. Springer, Cham, Switzerland.

Sándor, A.D., Kalmár, Z., Matei, I., Ionică, A.M., Mărcuţan, I.-D., 2017. Urban breeding corvids as disseminators of ticks and emerging tick-borne pathogens. Vector Borne Zoonotic Dis. 17, 152–154. https://doi.org/10.1089/vbz.2016.2054.

Sándor, A.D., Mărcuţan, D.I., D'Amico, G., Gherman, C.M., Dumitrache, M.O., Mihalca, A.D., 2014. Do the ticks of birds at an important migratory hotspot reflect the seasonal dynamics of *Ixodes ricinus* at the migration initiation site? A case study in the Danube Delta. PLoS One 9, e89378. https://doi.org/10.1371/journal.pone.0089378.

Sands, A.F., Apanaskevich, D.A., Matthee, S., Horak, I.G., Harrison, A., Karim, S., et al., 2017. Effects of tectonics and large-scale climatic changes on the evolutionary history of *Hyalomma* ticks. Mol. Phylogen. Evol. 114, 153–165. https://doi.org/10.1016/j.ympev.2017.06.002.

Santos-Silva, M.M., Beati, L., Santos, A.S., De Sousa, R., Núncio, M.S., Melo, P., et al., 2011. The hard-tick fauna of mainland Portugal (Acari: Ixodidae): An update on geographical distribution and known associations with hosts and pathogens. Exp. Appl. Acarol. 55, 85–121. https://doi.org/10.1007/s10493-011-9440-x.

Santos-Silva, M.M., Sousa, R., Santos, A.S., Melo, P., Encarnação, V., Bacellar, F., 2006. Ticks parasitizing wild birds in Portugal: detection of *Rickettsia aeschlimannii*, *R. helvetica* and *R. massiliae*. Exp. Appl. Acarol. 39, 331–338. https://doi.org/10.1007/s10493-006-9008-3.

Savitsky, B.P., 1963. Ecological and faunistic studies of blood-sucking arthropods in the foci of tick-borne encephalitis in Belarus and issues of healing the foci. PhD Thesis, Minsk University, Minsk, Belarus.

Schally, G., Csányi, S., Palatitz, P., 2022. Spring migration phenology of Eurasian woodcocks tagged with GPS-Argos transmitters in Central Europe. Ornis Fenn. 99, 104–116. https://doi.org/10.51812/of.121933.

Schulze, P., 1932. Die Zecken als Vogelparasiten. J. Ornithologie 80, 318–329.

Siuda, K., Majszyk, A., Nowak, M., 2006. Ticks (Acari: Ixodida) parasitizing birds (Aves) in Poland. Biol. Lett. 43, 2.

Siuda, K., Szymański, S., 1991. [A case of bringing along Mediterranean ticks *Ixodes* (*Ixodes*) *festai* Rondelli. 1926 (Acari: Ixodida: Ixodidae) to Poland by migrating birds]. Wiad. Parazytol 37, 25–29.

Skotarczak, B., Rymaszewska, A., Wodecka, B., Sawczuk, M., Adamska, M., Maciejewska, A., 2006. PCR detection of granulocytic *Anaplasma* and *Babesia* in *Ixodes ricinus* ticks and birds in west-central Poland. Ann. Agric. Environ. Med. 13, 21–23.

Spitalská, E., Literak, I., Kocianová, E., Taragel'ová, V., 2011. The importance of *Ixodes arboricola* in transmission of *Rickettsia* spp., *Anaplasma phagocytophilum*, and *Borrelia burgdorferi sensu lato* in the Czech Republic, Central Europe. Vector Borne Zoonotic Dis. 11, 1235–1241. https://doi.org/10.1089/vbz.2010.0210.

Spitalská, E., Literak, I., Sparagano, O.A.E., Golovchenko, M., Kocianová, E., 2006. Ticks (Ixodidae) from passerine birds in the Carpathian region. Wien Klin. Wochenschr. 118, 759–764. https://doi.org/10.1007/s00508-006-0729-4.

Subbotina, E.L., Loktev, V.B., 2012. [Molecular evolution of the tick-borne encephalitis and Powassan viruses]. Mol. Biol. (Moscow) 46, 82–92 (In Russian).

Sukhomlinova, O.I., 1977. [Ecology of ixodid ticks from small mammals in the Leningrad oblast]. Parazitologiya 11, 436–441 (In Russian).

Tamura, K., Stecher, G., Kumar, S., 2021. MEGA11: Molecular Evolutionary Genetics aAnalysis version 11. Mol. Biol. Evol. 38, 3022–3027. https://doi.org/10.1093/molbev/msab120.

Thompson, G.B., Arthur, D.R., 1955. VI. Records of ticks collected from birds in the British Isles. 2. Ann. Mag. Nat. Hist. 8, 57–60. https://doi.org/10.1080/00222935508651824.

Thompson, G.B., Arthur, D.R., 1956. XLIV. Records of ticks collected from birds in the British Isles. 3. Ann. Mag. Nat. Hist. 9, 385–390. https://doi.org/10.1080/00222935608655830.

Tiflova, L.A., Reznik, P.A., Ionova, E.V., 1970. [Ixodid ticks of Stavropol Krai and their medical significance. In: Vectors of Particularly Dangerous Infections and Their Control]. Stavropolskaya Pravda, Stavropol, Russia, pp. 459–471 (In Russian).

Toderas, I., Alekseev, N., Movila, A., Dubinina, H., Sapoval, A., 2008. Molecular identification of *Rickettsia japonica*, *Rickettsia helvetica* and *Babesia* sp. Eu1 in ticks collected from some bird species. Bul. Acad. Stiinte Mold. Stiint Vietii. 306, 91–97.

Tokarevich, N.K., Panferova, Y.A., Freylikhman, O.A., Blinova, O.V., Medvedev, S.G., Mironov, S.V., et al., 2019. *Coxiella burnetii* in ticks and wild birds. Ticks Tick Borne Dis. 10, 377–385. https://doi.org/10.1016/j.ttbdis.2018.11.020.

Toma, L., Liberato, C.D., Magliano, A., Montemaggiori, A., Luca, M.D., Piras, P.M., 2014. Recenti segnalazioni di *Ixodes festai* in Sardegna (Ixodida, Ixodidae). Boll. Assoc. Romana Entomol. 69, 1–5.

Touati, L., Figuerola, J., Alfarhan, A.H., Samraoui, B., 2015. Distribution patterns of ectoparasites of glossy ibis (*Plegadis falcinellus*) chicks. Zool. Ecol. 25, 46–53.

Tovornik, D., 1991. Data on ticks *Ixodes frontalis* (Panzer, 1798) and *Ixodes arboricola* Schulze et Schlottke, 1929, found on birds in Yugoslavia. Biol. Vestn. 39, 157–164.

Trilar, T., 2004. Ticks (Acarina: Ixodidae) on birds in Slovenia. Acrocephalus 25, 213–216.

Tsapko, N.V., 2017. Ticks (Acari, Ixodidae) of the north Caucasus: Species diversity and host-parasite relationships. Entomol. Rev. 97, 542–553. https://doi.org/10.1134/S0013873817040157.

Tsapko, N.V., 2023. [The role of corvids in the feeding of ixodid ticks (Acarina, Ixodidae) in the North Caucasus]. Russ. Ornithol. Zurnal 32, 156–160 (In Russian).

Tsapko, N.V., Kotti, B.K., 2017. [The tick *Ixodes frontalis* (Acari, Ixodidae) in the north Caucasus]. Parazitologiya 51, 253–260 (In Russian).

Turcek, F., 1953. Fauno-ecological investigations on *Ixodes* in Slovakia in 1953. Biologia 9, 464–468.

Van Oosten, A.R., Heylen, D.J.A., Matthysen, E., 2014. Host specificity of a bird-specialised endophilic ectoparasite, the tree-hole tick *Ixodes arboricola*. Parasitol. Res. 113, 4397–4405. https://doi.org/10.1007/s00436-014-4116-1.

Vial, L., Stachurski, F., Leblond, A., Huber, K., Vourc'h, G., René-Martellet, M., et al., 2016. Strong evidence for the presence of the tick *Hyalomma marginatum* Koch, 1844 in southern continental France. Ticks Tick Borne Dis. 7, 1162–1167. https://doi.org/10.1016/j.ttbdis.2016.08.002.

Voltsyt, O.V., 1997. [New faunistic records of ixodid ticks from eastern regions of Russia based in collections of the Zoological Museum of Moscow State University. Description of the nymph *Ixodes* (*Monoindex*) *maslovi*]. Parazitologiya 31, 265–268 (In Russian).

Walter, G., Massa, R., 1987. Ein Beitrag zur Ektoparasitenfauna der Zugvögel in Norditalien1. J. Appl. Entomol. 103, 523–527. https://doi.org/10.1111/j.1439-0418.1987.tb01018.x.

Wilhelmsson, P., Jaenson, T.G.T., Olsen, B., Waldenström, J., Lindgren, P.-E., 2020. Migratory birds as disseminators of ticks and the tick-borne pathogens *Borrelia* bacteria and tick-borne encephalitis (TBE) virus: A seasonal study at Ottenby Bird Observatory in south-eastern Sweden. Parasites Vectors 13, 607. https://doi.org/10.1186/s13071-020-04493-5.

Wodecka, B., Rymaszewska, A., Skotarczak, B., 2024. Host and pathogen DNA identification in blood meals of nymphal *Ixodes ricinus* ticks from forest parks and rural forests of Poland. Exp. Appl. Acarol. 62, 543–555. https://doi.org/10.1007/s10493-013-9763-x.

Yakimenko, V.V., Malkova, M.G., Shpynov, S.N., 2013. [Ixodid Ticks of Western Siberia]. Izdatel'skij Centr "Omskij nauchnyj vestnik. Omsk (In Russian).

Yang, Y., Tong, J., Ruan, H., Yang, M., Sang, C., Liu, G., et al., 2021. Genetic diversity of hard ticks (Acari: Ixodidae) in the south and east regions of Kazakhstan and northwestern China. Korean J. Parasitol. 59, 103–108. https://doi.org/10.3347/kjp.2021.59.1.103.

Yohannes, E., Biebach, H., Nikolaus, G., Pearson, D.J., 2009. Migration speeds among eleven species of long-distance migrating passerines across Europe, the desert and eastern Africa. J. Avian Biol. 40, 126–134. https://doi.org/10.1111/j.1600-048X.2008.04403.x.

Zając, Z., Kulisz, J., Kunc-Kozioł, R., Woźniak, A., Filipiuk, M., Rudolf, R., et al., 2022. Tick infestation in migratory birds of the Vistula river valley, Poland. Int. J. Environ. Res. Pub. Health 19, 13781. https://doi.org/10.3390/ijerph192113781.

Žėkienė, A., Paulauskas, A., Radzijevskaja, J., Jusys, V., 2011. Molecular investigation of tick-borne pathogens in ticks collected on migratory birds in Lithuania. Biologija 57, 4. https://doi.org/10.6001/biologija.v57i4.1927.

Zhang, Y.-K., Zhang, X.-Y., Liu, J.-Z., 2019. Ticks (Acari: Ixodoidea) in China: Geographical distribution, host diversity, and specificity. Arc. Insect Biochem. Physiol. 102, e21544 https://doi.org/10.1002/arch.21544.

Zolotarev, N.A., 1956. [The importance of wild birds of Dagestan in the development of ticks of the superfamily Ixodidae]. Trudy Instituta Zhivotnovodstva AN SSSR Mahachkala 4, 227–248 (In Russian).