INVESTIGATIONS OF THE ROLE OF BIRDS IN THE EPIDEMIOLOGY OF TICK-BORNE AND VECTOR-BORNE PATHOGENS

PhD dissertation

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List of abbreviations

ACC GEN	*Accipiter gentilis*
ACR ARU	*Acrocephalus arundinaceus*
ACR MEL	*Acrocephalus melanopogon*
ACR RIS	*Acrocephalus palustris*
ACR SCH	*Acrocephalus schoenobaenus*
ACR SCI	*Acrocephalus scirpaceus*
AEG CAU	*Aegithalos caudatus*
ANT TRI	*Anthus trivialis*
ASI OTU	*Asio otus*
CAR CHL	*Chloris chloris*
CER BRA	*Certhia brachydactyla*
COC COC	*Coccothraustes coccothraustes*
COR NIX	*Corvus cornix*
COT COT	*Coturnix coturnix*
DEN MAJ	*Dendrocopos major*
DEN MIN	*Dendrocopos minor*
EMB CIT	*Emberiza citrinella*
EMB SCH	*Emberiza schoeniclus*
ERI RUB	*Erithacus rubecula*
FIC ALB	*Ficedula albicollis*
FIC HYP	*Ficedula hypoleuca*
FRI COE	*Fringilla coelebs*
FRI MON	*Fringilla montifringilla*
GAR GLA	*Garrulus glandarius*
HIR RUS	*Hirundo rustica*
HYP ICT	*Hippolais icterina*
LUS SVE	*Luscinia svecica*
LAN COL	*Lanius collurio*
LOC FLU	*Locustella fluviatilis*
LOC LUS	*Locustella luscinioides*

LUS LUS	*Luscinia luscinia*
LUS MEG	*Luscinia megarhynchos*
PAN BIA	*Panurus biarmicus*
PAR CAE	*Cyanistes caeruleus*
PAR MAJ	*Parus major*
PAS MON	*Passer montanus*
PHO PHO	*Phoenicurus phoenicurus*
PHY COL	*Phylloscopus collybita*
PHY TRO	*Phylloscopus trochilus*
POR ANA	*Porzana porzana*
PRU MOD	*Prunella modularis*
PIC VIR	*Picus viridis*
PYR PYR	*Pyrrhula pyrrhula*
RAL AQU	*Rallus aquaticus*
REG REG	*Regulus regulus*
REM PEN	*Remiz pendulinus*
RIP RIP	*Riparia riparia*
SIT EUR	*Sitta europaea*
STU VUL	*Sturnus vulgaris*
SYL ATR	*Sylvia atricapilla*
SYL BOR	*Sylvia borin*
SYL COM	*Curruca communis*
SYL CUR	*Curruca curruca*
SYL NIS	*Curruca nisoria*
TRO TRO	*Troglodytes troglodytes*
TUR ILI	*Turdus iliacus*
TUR MER	*Turdus merula*
TUR PHI	*Turdus philomelos*
TUR TOR	*Turdus torquatus*
STR ALU	*Strix Aluco*
A	adult OR above ground (depends on context)
F	forest OR female (depends on context)

G	ground
L	larva
LDM	long-distance migrant
M	meadow OR male (depends on context)
MDM	middle-distance migrant
N	nymph
NA	no data available
R	resident OR reed (depends on context)
RSN	relative semimonthly numbers
SDM	short-distance migrant

1. Summary

The role of birds in the dispersal of ticks, other ectoparasitic vectors, and vector-borne pathogens has been the subject to extensive research. In Hungary, several studies have been carried out over the past decades to explore these dynamics. This thesis aims to provide a better understanding of the role birds play in the epidemiology of pathogens transmitted by ticks and other blood-feeding parasites. To gain a comprehensive understanding of this process, it is equally important to explore both the interactions between birds and blood-feeding vectors, and the potential vector roles of these arthropods. This thesis is based on five peer-reviewed articles published in scientific journals (listed in point ‘a’ of Chapter 8). To provide a more comprehensive overview, the thesis also incorporates findings from an unpublished study focusing on selected pathogens identified in avian louse flies.

A comprehensive review was conducted to assess the composition and size of the tick fauna infesting European birds. Over 200 published studies were analysed for this purpose. Based on our findings, 37 tick species have been identified so far on European birds, belonging to 16 different orders. Five widely distributed tick species—*Ixodes arboricola*, *Ixodes frontalis*, *Ixodes ricinus*, *Haemaphysalis concinna*, and *Hyalomma marginatum*—were further analysed for their host associations, revealing clear preferences for certain bird species based on ground-feeding behaviour and habitat use.

Following this, independent research took place examining the temporal relationship between birds and ticks. Ticks, collected from birds captured for ringing purposes at the Ócsa bird observatory between March 2014 and November 2022 were analysed. A total of 5,833 ticks from 10 species were collected from 2,395 infested birds. The dominant tick species were *I. ricinus* and *H. concinna*. *I. ricinus* was more common on ground-feeding, resident, and short-distance migratory birds in forest habitats, while *H. concinna* was found more frequently on long-distance migrants in reed habitats. Seasonal patterns showed that *I. ricinus* nymphs peaked in spring, larvae in autumn, while both larval and nymph stages of *H. concinna* peaked in summer. This study represents the first long-term bird-tick investigation in Central Europe, highlighting how bird ecology and tick life cycles jointly influence the spread of ticks. Notably, the Savi's Warbler (*Locustella luscinioides*) was identified as a key host for *H. concinna* in the region.

Parallel to the temporal distribution, the spatial distribution of ticks feeding on birds in Hungary was also studied. Ticks were collected from 38 species of passerine birds at seven locations in Hungary, resulting in 956 ixodid ticks. The most common species were *I. ricinus*, *H. concinna* and *I. frontalis*. Interestingly, 12 *Hyalomma* ticks (11 engorged nymphs, and one non-engorged

larva) were identified as *H. rufipes* based on three mitochondrial markers. This species was only found in the western and southeastern regions of Hungary. This study represents the first European observation of a reproducing *H. rufipes* population and offers a new ornithological explanation for its century-long presence in the Transdanubian region of the Carpathian Basin.

In the Carpathian Basin, *H. concinna*, one of the most common bird parasites in Hungary, occurs in unusually high numbers compared to other European countries. To gain a deeper understanding of the prevalence of piroplasms in these ticks and their potential role as vectors, we examined ticks collected from vegetation. Our study identified 11 distinct *Babesia* genotypes and *Theileria capreoli* within the *H. concinna* population. The results revealed that the peak monthly prevalence of *Babesia* and *Theileria* spp. in questing *H. concinna* ticks may not align with the peak abundance of the ticks themselves. This discrepancy may be influenced by factors such as changes in metabolism, behavior, and the survival rate of infected ticks. Further research is needed to clarify these observations.

In addition to ticks, our research also examined avian louse flies (Hippoboscidae: Ornithomyinae). We confirmed the presence of nine bird-specific hippoboscid species in Hungary, including *Ornithoctona laticornis*, an African tick species, which we identified in Europe for the first time. In several louse fly species, we discovered multiple *Trypanosoma* genotypes, which had not been previously reported in avian louse flies. Furthermore, we identified a strain of *Anaplasma phagocytophilum* in *Ornithomya avicularia*, a strain that, according to current knowledge, likely only infects birds. Additionally, the emerging pathogen *Haematospirillum jordaniae* was detected in three specimens of *Ornithomya fringillina*, marking the first report of this pathogen in hippoboscid flies.

2. Literature review

The role of birds in the transportation of arthropods with vector potential is long- known [1]. This aspect of bird life as parasite hosts is suspected to become more and more important due to the changes of ecological conditions, which may be a consequence of the currently ongoing climate change [2].

Hard ticks (Acari: Ixodidae) are common carriers of pathogens that can affect both humans and animals, so it is not surprising that they are considered one of the world's most important arthropod vectors [3]. Because of this, research on their ecology and distribution is of utmost importance [4]. This is especially true nowadays, as ecological systems are transforming rapidly due to climate change [5]. In the temperate zone of Europe, pathogens transmitted by hard ticks are responsible for the majority of the vector-borne diseases [6]. On this continent approximately 55 ixodid species occur [7]. From among these, the number of tick species that are regarded as indigenous will likely increase in several countries, in part due to climate change and the emergence of new, thermophilic tick species from the south.

In this scenario, the first prerequisite for the establishment of new tick species in any region is their (repeated) introduction, for which a very important natural route is via bird migration. Migratory birds are long-known carriers of ticks, most importantly *Hyalomma* species, from the south to temperate regions of Europe [8], even its northernmost parts [9]. However, birds usually carry immature ticks, larvae and nymphs of *Hyalomma* species [10], therefore in case of these thermophilic ticks, another crucial prerequisite prior to establishment is the ability of nymphs detaching from birds to moult to adults. This was already reported for both *Hyalomma marginatum* and *Hyalomma rufipes* from several countries north of the Mediterranean Basin, as exemplified by the UK [11], and the Netherlands [12] in western Europe, Sweden in northern Europe [13] or Hungary in central Europe [14]. Consequently, *Hyalomma* adults might also overwinter [15] In recent years these species have been reported in Europe with increasing numbers north of the Mediterranean Basin, and were even able to establish a resident population[2,14,16,17].

The emergence of *Hyalomma marginatum* was reported in a previously non-endemic region of the Mediterranean Basin in southern France, but it was stated that even in such newly invaded areas this tick species probably remains exclusively Mediterranean and cannot expand outside this climatic range [18]. On the other hand, north of the Mediterranean region, in the Carpathian Basin (geographically including both Hungary and the Transylvanian Basin: [19]), adult ticks from the genus *Hyalomma* are long-known for their autochthonous occurrence under continental climate. This was already reported in the 19th century [4], and later confirmed

[20,21]. At the same time, in the absence of detailed morphological description, the species in the Carpathian Basin remained uncertain, because some hints were more relevant to *H. rufipes* (e.g., the name *Hyalomma aegyptium*: [21]), while others to *H. marginatum* (as implied in the predominance of the species referred to from Hungary in the Mediterranean Basin: [20]). More recently, *H. rufipes* adults were found on cattle on two occasions in Hungary [14], and one adult on the same host species 10 years later by citizen science method [17].

Interestingly, these century-long reports on the presence of adult *Hyalomma* ticks in the Carpathian Basin attest that the chance for their occurrence is more likely in certain endemic areas of the country. However, this hypothesis was not yet tested from the point of view of bird migration, despite the long-known import of *Hyalomma* nymphs by birds into this geographical region [1].

The importance of synanthropic, resident bird species (e.g. the Blackbird (*Turdus merula*)) is also crucial, regarding the local dissemination of ticks, as they can introduce ticks to urban areas [22]. The monitoring of bird-tick relationships is a long-standing and intensively researched field that has greatly contributed to what is known about ticks and the epidemiology of the pathogens they transmit [23–25].

Research on this topic has been conducted in Hungary for decades, particularly at Ócsa Bird Ringing Station [2,26–30]. At this station more than 15 thousand birds are caught yearly. The area has several different habitat types (e.g. forest, arable field, reedbed) [31] and is an important stop-over site for birds migrating along the Adriatic Flyway through Central Europe. Therefore, it is suitable for the examination of both migratory and resident birds of different habitats.

Louse flies (Diptera: Hippoboscidae) are blood-sucking parasites of birds and mammals, with approximately 213 known species worldwide [32]. The family Hippoboscidae contains three subfamilies: Hippoboscinae, Lipopteninae and Ornithomyinae. Ornithophilic louse flies generally belong to the Ornithomyinae subfamily [33], however members of the Hippoboscinae subfamily (e.g. *Hippobosca equina* and *Hippobosca longipennis*) can also parasitize birds [34]. These parasites disturb their hosts with their presence, and also play an important role in the ecology of other parasites and may even contribute to their evolution by phoresis [35]. They can carry a multitude of different pathogens with high veterinary-medical significance, as exemplified by the West-Nile virus [36] and *Babesia* species [37], although their vector role is not yet clear. Research on hippoboscids is flourishing nowadays, i.e., their ecology, evolution, and potential role in the transmission of pathogens have recently become heavily investigated topics [32,38–43].

Although there are studies on louse flies originated from Central- [32] Northern- [43], Southern-[39], Western- [44], and Eastern Europe [45] as well, but only a few of them present long-term evaluations with continuous sample collection. Despite the fact, that research on avian ectoparasites has been increasingly conducted in Hungary and in other Central European countries, during the previous decade [2,26,28,32,41], studies on ornithophilic hippoboscids also appear to be neglected compared to other arthropod vectors that are generally considered epidemiologically more important (i.e., ticks and mosquitoes) [46,47]. Previous Hungarian studies on hippoboscids date back to the previous century, and to the Millenium [48,49]. In light of the above, research on these insects bears regional, as well as international importance.

3. Materials and methods

3.1 Databases used for systematic reviews, and the categorisation of birds

The primary corpus of publications used for writing chapter **4.1** was collated with database search using the following keywords: “ticks” OR “Ixodidae” OR “*Ixodes*” OR “*Hyalomma*” OR “*Haemaphysalis*” AND “birds” AND “Europe”, followed by a search with names of bird-specialist tick species (*Ixodes arboricola, Ixodes caledonicus*, *Ixodes eldaricus*, *Ixodes festai*, *Ixodes frontalis*, *Ixodes lividus*, *Ixodes rothschildi*, *Ixodes unicavatus* and *Ixodes uriae*). The following databases were used: Web of Science, Zoological Record, and Google Scholar. These records were imported into an Excel file, followed by screening the publications and references cited within. After exclusion of duplicates, we extracted each individual bird host-tick record from these references, noting the location (country), host and parasite species and developmental stage of ticks. *Ixodes redikorzevi* is considered as a synonym of *I. acuminatus.* Data were only included in the checklist if the tick collected from a bird was reported as identified to the species level.

In chapters **4.1 and 5.1**: Genus names are not abbreviated in the headings, owing to the high number and mixed usage of host and tick Latin names, also taking into account that scientists from a broad range of biology-related fields may use this checklist. Whenever a bird species was mentioned by its binominal name in an article, this was used for identification, even if the English name was also written in the text. English and Latin host species names are followed by tick developmental stages if this information was available (L: larva, N: nymph, M: male, F: female, A: adult [where there was no information about the sex of the adult tick)]. The abbreviation “NA” is used to indicate that no data were available about the sex and developmental stage of ticks collected from birds. If a tick species was reported from bird(s) in a country without mentioning avian host species, an exclamation mark (!) follows the country name in the list. If tick species infesting a certain bird species are mentioned in a reference but only some of the data inform about the tick developmental stage, only these were incorporated into the text. It is also noteworthy that in some reports blood meal analysis allowed the identification of previous tick hosts. In addition, data on ticks reported from bird nests are included and marked in the text as “in nest”: these ticks probably also originate from or can associate with birds. The geographical area covered by this review is in the Western Palearctic, excluding North Africa, the Middle East, Belarus and Russia but including Ukraine. Cyprus however, is also considered. Not just because it is partially European territory, but due to the fact that the island has a high epidemiological significance concerning the aim of this manuscript. Regarding geographical names, old references often refer to Czechoslovakia, which no longer exists. In cases when it was unambiguous whether the samples came from the Czech Republic or Slovakia, the country is mentioned as such. To maintain the user friendliness of this checklist the broader Palearctic distribution, general ecology, and vector role of tick species are not mentioned.

Birds were categorized according to their feeding place, minimum and maximum body mass, migration habits, and habitats according to ornithological data and previous reports [28,50,51]. In order to categorize birds according to their feeding places, “Above ground” category was created. Birds belonging to this group are feeding on (e.g.) reed trunks, bushes, or branches that do not touch the ground directly but are not far from it either. For this categorization, the expertise of our co-authors (Tibor Csörgő and Dávid Kováts) were used, as well as the available literature data [51]. Categorization of birds in the cases of **chapters 4.1 and 5.1** has been conducted by Attila D. Sándor and was based on his expertise and relevant literature data [52] (Supplementary Table 1, Supplementary Figure 1)

In some of the Figures and Tables presented in this study, HURING codes were used instead of the birds’ full English and/or binomial names. These abbreviations are clarified in the List of abbreviations paragraph and in Supplementary Table 2. English bird species names are capitalized, following international recommendations (https://bou.org.uk/britishlist/bird-names/).

3.2 Sample collection

3.2.1 Tick and louse fly collection from birds

Birds were caught and handled for the purpose of ringing. Birds were mist -netted by standard ornithological mist-nets (mesh size 16 mm) and were examined for the presence of ticks, between March and November. Ectoparasites were removed with the help of pointed tweezers and were placed and stored in 96% ethanol. Bird ringing and tick collection were constant from the beginning of March to the end of October each year. Only sporadic data were obtained from the other months. Birds were handled, identified, and released by professional ringers throughout our study. The numbers of negative birds were not always recorded due to the difficulties of field conditions.

For chapters 4.3 and 5.3: The sample collection took place between March 2022 and November 2022 and was conducted at multiple sites of Hungary, namely: (1) Tömörd Bird Ringing Station (coordinates: 47°21'N, 16°39'E), (2) Ócsa Bird Ringing Station (47°19'N, 19°13'E), (3) Bódva Valley Bird Ringing Station (coordinates: 48°27'N, 20°42'E), (4) Fenékpuszta Bird Ringing Station (46°44'N, 17°14'E), (5) Izsák, Lake Kolon Bird Ringing Station (coordinates: 46°46'N, 19°19'E), (6) Dávod, Lake Földvár Bird Ringing Station (coordinates: 46°0'N, 18°51'E), (7) Lake Fehér Ornithology Camp (coordinates: 46°20'N, 20°6'E).

For chapters 4.2 and 5.2: The sample collection period took place between March 2015 and November 2022 and was conducted at Ócsa Bird Ringing Station (47°19'N, 19°13'E). The ticks collected at this station in 2022 are evaluated in chapters **4.3** and **5.3** as well.

For **chapters 4.5 and 5.5**, louse flies were collected parallelly to the previously mentioned tick collections. Some flies were collected from Hooded crows (*Corvus cornix*) by licensed hunters as well. Based on personal communication, collecting louse flies is difficult and not always successful. This may affect subsequent calculations.

In **chapters 4.6 and 5.6**, In addition to some of the louse flies examined in chapters **4.5** and **5.5**, additional louse flies were collected at the previously mentioned collection sites, and at other locations in Hungary, namely: Gárdony-Dinnyés (47°10'N, 18°33'E), Sumony (45°58'N, 17°53'E), Patak (48°1'N, 19°8'E). At these sites, sample collections were continuous from March 2023 until November 2024 as well. As the aim of this study was to find pathogens in different bird louse species, other specimens from the collection of the Department of Parasitology and Zoology, Veterinary Medicine, Budapest were also analysed. This included louse flies collected occasionally at several other locations in Hungary during bird ringing, or veterinary-related procedures. Some samples from Norway (three specimens of *Ornithomya chloropus*) and from Malta (one *Ornithophila metallica* and six *Ornithomya biloba*) were also evaluated. In this study, louse flies were only analysed, if phoresy was not detected on them, to avoid potential bias. In the cases of three specimens of *O. biloba* from Malta, mites present on their wings were accurately removed.

3.2.3 Tick collection from the vegetation

Haemaphysalis concinna specimens examined in **chapters 4.4 and 5.4** were collected between February 2019 and November 2020. The tick collection site was chosen based on the results of a large-scale survey of urban biotopes in Budapest [53]. This biotope is part of a large cemetery, where neglected parts had dense lower vegetation covering [grass, weeds and nearly continuous ivy (Hedera sp.)] and sparse distribution of bushes and trees. This site was visited at monthly intervals, at the end of each month. Tick collections were performed under dry weather conditions. Ticks were collected from the vegetation by the dragging-flagging method, i.e., a white towel, measuring 1×1 m, was drawn over the vegetation and checked every 10 s. During this the same five, approx. 60 m long parallel transects were sampled regularly (i.e., 300 m^2). Ticks attached to and removed from the collecting device were immediately put into and stored in 96% ethanol.

3.3 Morphological identification of tick and louse fly species

Ticks and louse flies were identified with a stereomicroscope (SMZ-2 T, Nikon Instruments, Japan, illuminated with model 5000-1, Intralux, Switzerland). To identify *Ixodes ricinus, I. frontalis, I. lividus, I. arboricola,* and *Dermacentor reticulatus, Dermacentor marginatus, and H. inermis* to the species level and *Hyalomma* species to the genus level, we used morphological keys provided by Estrada-Peña et al. [7] *Hyalomma* ticks were identified to the species level with molecular methods [2]. Differentiation of subadults of *H. concinna* and *H. punctata* was based on the morphological keys by Filippova [54]**.** For the identification of *I. festai,* we used the manuscripts of Contini et al. [55] and Hornok et al. [46].

Louse fly species were identified based on standard taxonomic keys: [32,44,56]

3.4 DNA extraction and molecular analyses

Ticks and louse flies were treated individually during molecular analyses.

Ticks and louse flies were disinfected on their surface with sequential washing for 15 s in 10% NaClO or detergent, tap water and distilled water. DNA was extracted with the QIAamp DNA Mini Kit (QIAGEN, Hilden, Germany) according to the manufacturer's instruction, including an overnight digestion in tissue lysis buffer and Proteinase-K at 56 °C. Extraction controls (tissue lysis buffer) were also processed with the tick/hippoboscid samples to monitor cross-contamination.

For molecular identification of ticks, louse flies and pathogens, the target genes and the primers are enlisted in Table 1.

Table 1: Oligonucleotide sequences and cycle parameters of PCRs used in this dissertation.

Primer	Target group	Target gene (amplicon length)	Primers (5'-3')	Cycling conditions					
				initial denaturation	denaturation	annealing	extension	final extension	Number of cycles
[57]	**Ixodidae, barcode**	cox1 (710 bp)	LCO1490 (GGT CAA CAA ATC ATA AAG ATA TTG G) HCO2198 (TAA ACT TCA GGG TGA CCA AAA AAT CA)	95 °C, 5m	94 °C, 40s	48 °C, 1m	72 °C, 1m	72 °C, 10m	40
[58]	**Ixodidae, barcode**	16S rRNS (460 bp)	16S+1 (CTG CTC AAT GAT TTT TTA AAT TGC TGT GG) 16S-1 (CCG GTC TGA ACT CAG ATC AAG T)	95 °C, 5m	94 °C, 40s	51 °C, 1m	72 °C, 1m	72 °C, 10m	40
[59–61]	**Ixodidae, barcode**	12S rRNS (360 bp)	T1B (AAA CTA GGA TTA GAT ACC CT) T2A (AAT GAG AGC GAC GGG CGA TGT)	95 °C, 5m	94 °C, 30s	50 °C, 1m	72 °C, 30s	72 °C, 7m	5
					94 °C, 30s	53 °C, 1m	72 °C, 30s		30
[62]	**Piroplasms**	18S rRNS (500 bp)	BJ1 (GTC TTG TAA TTG GAA TGA TGG) BN2 (TAG TTT ATG GTT AGG ACT ACG)	95 °C, 10m	94 °C, 30s	54 °C, 30s	72 °C, 40s	72 °C, 5m	40
[63,64]	***Trypanosoma sp.***	ssu (800-1000 bp)	609F (CAC CCG CGG TAA TTC CAG C) 706Rnew (CTG AGA CTG TAA CCT CAA)	95 °C, 5m	94 °C, 40s	49 °C, 1.5m	72 °C, 1m	72 °C, 5m	40
[65]	**Rickettsiaceae**	gltA (380 bp)	RpCs.877p (GGG GGC CTG CTC ACG GCG G) RpCs.1258n (ATT GCA AAA AGT ACA GTG AAC A)	95 °C, 5m	94 °C, 20s	48 °C, 30s	72 °C, 1m	72 °C, 5m	40
[66,67]	***Bartonella sp.***	16S-23S ITS (600 bp)	Ba325s (CTT CAG ATG ATG ATC CCA AGC CTT CTG GCG) Ba1100as (GAA CCG ACG ACC CCC TGC TTG CAA AGC A)	95 °C, 5m	94 °C, 30s	65 °C, 30s	72 °C, 50s	72 °C, 5m	40
[68]	***Borrelia burgdorferi s.l.***	5S-23S IGS (450 bp)	B5Sborseq (GAG TTC GCG GGA GAG TAG GTT ATT GCC) B23Sborseq (TCA GGG TAC TTA GAT GGT TCA CTT CC)	94 °C, 5m	94 °C, 20s	70 °C, 30s (-1°C/cycle)	72 °C, 30s	72 °C, 7m	10
					94 °C, 20s	60 °C, 30s	72 °C, 30s		40
[69]	**Anaplasmataceae**	16S rRNS (350 bp)	EHR16SD (GGT ACC YAC AGA AGA AGT CC) EHR16SR (TAG CAC TCA TCG TTT ACA GC)	95 °C, 10m	95 °C, 30s	55 °C, 30s	72 °C, 45s	72 °C, 5m	40
*	**Anaplasmataceae**	16S rRNS (700 bp + 650 bp)	Ana16SF (TTA GTG GCA GAC GGG TGA GTA ATG) Ana16SMR (CTA CCA GGG TAT CTA ATC CTG TTT GC); Ana16SM (GCA AAC AGG ATT AGA TAC CCT GGT AG) Ana16SRR (TGA CGG GCA GTG TGT ACA AGA CCC GAG)	95 °C, 5m; 95 °C, 5m	95 °C, 30s; 95 °C, 30s	57 °C, 30s; 58 °C, 30s	72 °C, 1m; 72 °C, 1m	72 °C, 5m; 72 °C, 5m	40 40
[70]	***Anaplasma phagocytophilum***	GroEL (640 bp)	EphplGroEL(569)F (ATG GTA TGC AGT TTG ATC GC) EphplGroEL(1193)R (TCT ACT CTG TCT TTG CGT TC)	95 °C, 5m	95 °C, 30s	52 °C, 40s	72 °C, 1m	72 °C, 7m	40

*Primers designed by Prof. Sándor Hornok

In all PCRs non-template reaction mixture served as negative control. Extraction controls and negative controls remained PCR negative in all tests. Purification and sequencing of the PCR products were done by Biomi Ltd. (Gödöllő, Hungary). Quality control and trimming of sequences were performed with the BioEdit program, then alignment with GenBank sequences by the nucleotide BLASTN program (https://blast.ncbi.nlm.nih.gov).

3.5 Phylogenetic analyses

Sequences from other studies, used here for phylogenetic analyses, were retrieved from the GenBank database (https://www.ncbi.nlm.nih.gov/genbank/).

Analysis of piroplasms (chapters 4.4 and 5.4): The percentage of trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown below the branches [71]. All ambiguous positions were removed for each sequence pair (pairwise deletion option). There were a total of 445 positions in the final dataset. Phylogenetic analyses were conducted with the Neighbor-Joining method [72] and p-distance model [73] by using MEGA 11 [74].

Analysis of louse flies (chapters 4.5 and 5.5): The evolutionary history was inferred by using the Maximum Likelihood method and General Time Reversible (GTR) model [73] The percentage of trees in which the associated taxa clustered together is shown below the branches. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. This analysis involved 46 nucleotide sequences. There were a total of 589 positions in the final dataset. Evolutionary analyses were conducted in MEGA11 [74].

Analysis of pathogens in chapters 4.6 and 5.6: The best fitting evolutionary models were chosen with the help of the program IQTREE2 (version 2.4.0) [75].

Analysis of Trypanosoma species: The evolutionary history was inferred by using the Maximum Likelihood method and Tamura 3-parameter model [76]. The tree with the highest log likelihood (-2181.24) is shown. The percentage of trees in which the associated taxa clustered together is shown below the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Tamura 3 parameter model, and then selecting the topology with superior log likelihood value. The rate variation model allowed for some sites to be evolutionarily invariable ([+*I*], 42.22% sites). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. This analysis involved 36 nucleotide sequences. There were a total of 829 positions in the final dataset. Evolutionary analyses were conducted in MEGA11 [74].

Analysis of Anaplasma species: The evolutionary history was inferred by using the Maximum Likelihood method and Tamura-Nei model [77]. The tree with the highest log likelihood (-1638.77) is shown. The percentage of trees in which the associated taxa clustered together is shown below the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Tamura-Nei model, and then selecting the topology with superior log likelihood value. A discrete Gamma distribution was used to model evolutionary rate differences among sites (4 categories (+*G*, parameter = 0.4607)). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. This analysis involved 36 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. There were a total of 445 positions in the final dataset. Evolutionary analyses were conducted in MEGA11 [74].

3.6 Statistical analyses

Data curation and calculation of prevalences, mean and median tick intensity was done in Microsoft Office Excel. Mean and median intensities were calculated for each parasite (and developmental stages) according to Reiczigel et al.[78].

Fisher's exact test was used:

- To conduct the statistical comparisons in **chapters 4.1 and 5.1** (program used: https://www.langsrud.com/fisher.htm).
- In **chapters 4.2 and 5.2** to compare the host attributes (habitat, migratory habit, feeding place) of *I. ricinus* and *I. frontalis* (program used: R -program v. 4.3.0.) [79].
- For the comparisons in **chapters 4.3 and 5.3** (program used: https://www.langsrud.com/fisher.htm)
- In **chapters 4.4 and 5.4** to compare the seasonal *Theileria capreoli* prevalences and *Babesia* prevalences of each "predictor months" (May and July) to all "non-predictor months" together (March, April, June, August, September, October, November). In these chapters, larvae (which typically show aggregated presence during questing activity, originating from the same egg clutch, and were not distributed by hosts before) were excluded from statistical analyses (program used: R-program v. 4.3.1) [79].
- In **chapters 4.5 and 5.5**, for the comparison of host attributes (habitat, migratory habit, feeding place), Fisher's exact tests were used (program used: R-program v. 4.3.0) [79].
- In **chapters 4.6 and 5.6**, Fisher's exact tests were used for the comparison of the numbers of *O. avicularia* and *O. turdi* individuals that were co-feeding with ticks (program used: R-program v. 4.3.1) [79].

Chi-squared test was used for comparing the half-yearly activity of *I. ricinus* larvae and nymphs, and the migration habits, habitats and the feeding places of the hosts of *I. ricinus* and *H. concinna* **(chapters 4.2 and 5.2).**

Results were considered significant if $p<0.05$.

The average body mass of each bird species was calculated as the mean of the minimum and the maximum body mass registered and listed Supplementary Table 2 (Average body mass= $\frac{\text{Minimum body mass+Maximum body mass}}{2}$).

The mean intensity of *H. concinna* and *I. ricinus* infestation was calculated for each group. The results are shown in Figure 3. Intensity was only calculated if there were 10 or more infested birds in the respective category, to minimize the distortion caused by outliers. Data from one group (<=10g Average body mass for *H. concinna)* was therefore excluded ($n_{\text{birds}}=2$).

In Supplementary Figure 2, Relative, semimonthly numbers (RSN) were calculated as follows:

$$\text{RSN} = \frac{\text{SMN}}{\text{MON}} \text{ X } 100$$

(SMN= Semimothly number of the tick species and stage; MON = number of the tick species and stage from the respective year, between March 01- October 31)

4. Results

4.1 Hard ticks (Acari: Ixodidae) associated with birds in Europe: review of literature data

PROSTRIATA

Ixodes acuminatus

Overview:

Ixodes acuminatus is distributed in temperate and Mediterranean Europe [7]. Accordingly, this tick species is occasionally found on birds in South-European countries. Based on literature data it is mainly a parasite of passeriform birds (from this order 15 species have been shown as hosts) but has also been found twice on galliform birds.

Passeriformes: 15; Galliformes: 2

Hosts:

- Bearded reedling – *Panurus biarmicus* (**N:** [80])
- Common blackbird – *Turdus merula* (**F:** [81], [82], [23]; **NA:** [83], [84])
- Common chaffinch – *Fringilla coelebs* (**L:** [81]**;** **N:** [81])
- Common pheasant – *Phasianus colchicus* (**A:** [85])
- Common redstart – *Phoenicurus phoenicurus* (**L:** [81])
- Eurasian blue tit- *Cyanistes caeruleus* (**N:** [81])
- Eurasian magpie – *Pica pica* (**L:** [81]**;** **N:** [81])
- European goldfinch – *Carduelis carduelis* (**F:** [81])
- European robin – *Erithacus rubecula* (**N:** [80])
- Fieldfare -*Turdus pilaris* (**NA:** [81])
- Garden warbler – *Sylvia borin* (**N:** [86])
- Great tit – *Parus major* (**L:** [81]**;** **N:** [80]**,** [81])
- House sparrow – *Passer domesticus* (**NA:** [81])
- Red-legged partridge – *Alectoris rufa* (**A:** (19))
- Redwing – *Turdus iliacus* (**N:** [87])
- Song thrush – *Turdus philomelos* (**F:** [23])
- Winter wren – *Troglodytes troglodytes* (**L:** [87]**;** **N:** [87])

Distribution of reported cases: Greece [86], Italy [85] [88]**!, Romania** [80] [81] [89]**!, Cyprus** [23], **Portugal** [82] [83] [87]**, France** [84]

Ixodes arboricola

Overview:

Ixodes arboricola is widespread throughout Europe. As its English name suggests, the Tree-hole tick is primarily a parasite of hole-nesting birds [7]. Literature data usually support this theory, as *I. arboricola* was mostly found on passeriform (35 species), strigiform (5 species), piciform (1 species), and columbiform (1 species) birds. The fact that other, non-hole-nesting predators (2 falconiform and 1 accipitriform species) have been described as hosts, does not contradict the former statement, as these species can become infected with ticks by getting in contact with their prey.

Passeriformes: 34; Strigiformes: 5; Falconiformes: 2; Columbiformes: 1; Piciformes: 1; Accipitriformes: 1

Hosts:

- Barn owl – *Tyto alba* (**L:** [90]; **NA:** [91], [92])
- Barn swallow – *Hirundo rustica* (**NA:** [92])
- Boreal owl – *Aegolius funereus* (**N:** [93] **in nest**)
- Coal tit – *Periparus ater*(**N:** [94]; **NA:** [92], [95], [96])
- Collared flycatcher – *Ficedula albicollis* (**N:** [97], [98]; **M:** [97], [98]**in nest; F:** [98], [98][a]**; NA:** [99])
- Common blackbird – *Turdus merula* (**L:** [82]; **N:** [81], [100], [80]; **NA:** [96], [101])
- Common kestrel- *Falco tinnunculus* (**F:** [100])
- Common redstart – *Phoenicurus phoenicurus* (**L:** [81], [97]; **N:** [81]; **NA:** [99])
- Common starling – *Sturnus vulgaris* (**L:** [97], [100], [9], [102]; **N:** [97], [100], [9], [102]; **M:** [102]; **F:** [97], [100], [9], [102]; **NA:** [81], [92], [99], [96], [103][a] **in nest,**)
- Common wood pigeon – *Columba palumbus* (**L:** [100])
- Eurasian blue tit- *Cyanistes caeruleus* (**L:** [81], [94], [104], [105], [106], [107]; **N:** [80], [82], [94], [97], [105], [106], [107], [108], [109], [110]; **M:** [98]**in nest; F:** [97], [98], [108], [105], [107]; **NA:** [83], [91], [95], [99], [103], [111])
- Eurasian bullfinch – *Pyrrhula pyrrhula* (**NA:** [96])
- Eurasian jay – *Garrulus glandarius* (**A:** [112])
- Eurasian nuthatch – *Sitta europaea* (**L:** [87], [111]; **N:** [87], [94], [110], [111], [112]; **A:** [111]; **M:** [98]**in nest; NA:** [92], [95], [99], [113])
- Eurasian penduline tit – *Remiz pendulinus* (**L:** [114]i**n nest**)

- Eurasian pygmy owl – *Glaucidium passerinum* (**L:** [97])
- Eurasian reed warbler – *Acrocephalus scirpaceus* (**NA:** [96])
- Eurasian siskin – *Carduelis spinus*(**N:** [106])
- Eurasian tree sparrow – *Passer montanus* (**NA:** [92], [96], [103])
- Eurasian treecreeper – *Certhia familiaris* (**L:** [99], **NA:** [95])
- European greenfinch – *Carduelis chloris* (**L:** [107])
- European pied flycatcher – *Ficedula hypoleuca* (**N:** [97], [110]; **NA:** [96], [103])
- European robin – *Erithacus rubecula* (**L:** [80], [81]; **N:** [115], [81], [80], [94], [97]; **NA:** [96])
- European serin – *Serinus serinus* (**N:** [87]; **F:** [87])
- Great spotted woodpecker – *Dendrocopos major* (**NA:** [112])
- Great tit – *Parus major* (**L:** [81], [94], [97], [100], [9], [105], [106], [107], [109], [116], [117]; **N:** [80], [81], [82], [83], [87], [90], [94], [97], [98], [100], [9], [105], [106], [107], [108], [110], [116], [117]; **M:** [98][a]**in nest; F:** [90], [98], [98][a], [105], [106], [108], [118], [119]; **NA:** [83], [91], [95], [99], [103], [111])
- House sparrow – *Passer domesticus* (**NA:** [92], [96])
- Little owl – *Athene noctua* (**N:** [100]; **F:** [100]; **NA:** [96])
- Long-tailed tit – *Aegithalos caudatus* (**L:** [87])
- Marsh tit – *Poecile palustris* (**L:** [94], [107]; **N:** [107]; **NA:** [95], [96])
- Northern goshawk – *Accipiter gentilis* (**L:** [100])
- Peregrine falcon – *Falco peregrinus* (**L:** [120]; **N:** [120]; **F:** [120])
- Rook – *Corvus frugilegus* (**L:** [121])
- Sand martin – *Riparia riparia* (**N:** [90]**in nest; F:** [90]**in nest**; **NA:** [96])
- Short-toed treecreeper – *Certhia brachydactyla* (**L:** [82]; **NA:** [83])
- Song thrush – *Turdus philomelos* (**L:** [80]; **N:** [115], [80])
- Spotless starling – *Sturnus unicolor* (**L:** [83]; **NA:** [83])
- Spotted flycatcher – *Muscicapa striata* (**N:** [81]; **F:** [97],)
- Tawny owl -*Strix aluco* (**L:** [97]; **NA:** [92])
- Western jackdaw – *Corvus monedula* (**L:** [121]; **N:** [97]; **F:** [97]; **NA:** [96], [113])
- Willow tit – *Poecile montana* (**N:** [106]; **NA:** [96])
- Willow warbler – *Phylloscopus trochilus* (**NA:** [96])
- Winter wren – *Troglodytes troglodytes* (**N:** [106]; **NA:** [96])
- Yellowhammer – *Emberiza citrinella* (**NA:** [91])

Distribution of reported cases: Sweden [97] [9] [122]**!, United Kingdom** [90] [91] [96] [111] [119]**, Czech Republic** [94] [95] [98] [123]**!, Slovakia** [92] [98][a] [99] [114]**, Netherlands** [108]**, Denmark** [102]**, Norway** [115]**, Belgium** [105] [110] [113] [116]**, Romania** [81] [80]

[89]**!** [121]**, Ukraine** [118]**, Portugal** [82] [83] [87]**, Poland** [92] [106] [117]**, Spain** [107] [109]**, Switzerland** [100]**, Germany** [103] [120]**, Hungary** [112]**, Croatia** [101]**, Belarus** [103][a]

Ixodes berlesei

Overview: According to literature data, *I. berlesei* was reported from birds in France. Unfortunately, the source article [84] is not accurate about the host species, but we do know that they belong to the Columbiformes order.

Columbiformes:1

Distribution of reported cases: France [84]**!**

Ixodes caledonicus

Overview: *Ixodes caledonicus* is an ornithophilic tick species [124]. It is primarily a parasite of the northern European bird fauna. Despite the limited data available, the host range appears to be broad: it has been reported from 6 passeriform, 3 falconiform, 1 caprimulgiform, and one procellariiform bird species.

Passeriformes: 6; Falconiformes: 3; Caprimulgiformes: 1; Procellariiformes: 1; Columbiformes: 1

Hosts:

- Common kestrel- *Falco tinnunculus* (**NA:** [96])
- Common redstart – *Phoenicurus phoenicurus* (**N:** [90])
- Common starling – *Sturnus vulgaris* (**NA:** [96])
- Common swift – *Apus apus* (**NA:** [92])
- Gyrfalcon – *Falco rusticolus* (**L:** [125]**; N:** [125]**; A:** [125]**; NA:** [96])
- Hooded crow – *Corvus cornix* (**NA:** [96])
- Northern fulmar – *Fulmarus glacialis* (**F:** [126]**; NA:** [96])
- Northern raven – *Corvus corax* (**NA:** [96])
- Peregrine falcon – *Falco peregrinus* (**N:** [97])
- Red crossbill – *Loxia curvirostra* (**NA:** [96])
- Rock dove – *Columba livia* (**NA:** [126][a])
- Western jackdaw – *Corvus monedula* (**NA:** [96])

Distribution of reported cases: United Kingdom [96] [90]**, Faroe Islands** [126]**, Sweden** [97]**, Poland** [92]**, Norway** [96]**!, Germany** [96]**!, Iceland** [125]**, NA** [126][a]

Ixodes canisuga

Overview: *Ixodes canisuga* is primarily a parasite of mammals [7] and it is relatively rare on birds. So far, it has been found on 5 passeriform and on 2 strigiform hosts.

Passeriformes: 5; Strigiformes: 2

Hosts:

- Common starling – *Sturnus vulgaris* (**NA:** [96])
- Eurasian blue tit- *Cyanistes caeruleus* (**NA:** [96])
- Eurasian eagle-owl – *Bubo bubo* (**N:** [127])
- Eurasian tree sparrow – *Passer montanus* (**NA:** [96])
- Great tit – *Parus major* (**NA:** [96])
- Little owl – *Athene noctua* (**L:** [90]**; N:** [90]**; F**: [90])
- Sand martin – *Riparia riparia* (**M:** [90]**in nest; F:** [90]**in nest**)

Distribution of reported cases: United Kingdom [90] [96]**, Germany** [128]**!, Portugal** [127]

Ixodes eldaricus

Overview: *Ixodes eldaricus* is a rare, poorly known tick species. The only available data about this parasite feeding on European birds are from Poland and Cyprus, where this tick species was reported from four passeriform bird species in total

Passeriformes: 4

Hosts:

- Common blackbird – *Turdus merula* (**N:** [23])
- Dunnock – *Prunella modularis* (**F:** [129])
- European robin – *Erithacus rubecula* (**M:** [129]**; F:** [129])
- Tree pipit – *Anthus trivialis* (**N:** [23])

Distribution of reported cases: Poland [129]**, Cyprus** [23]

Ixodes festai

Overview: *Ixodes festai* is a poorly known species that was reported from 5 passeriform birds, mostly in Central European countries.

Passeriformes: 5

Hosts:

- Common blackbird – *Turdus merula* (**N:** [100]**; F:** [100], [117], [130]**; NA:** [55])
- Common chaffinch – *Fringilla coelebs* (**F:** [100])
- Dunnock – *Prunella modularis* (**N:** [100]**; F:** [46])
- European greenfinch – *Carduelis chloris* (**F:** [46])
- Song thrush – *Turdus philomelos* (**M:** [55]**; F:** [130], [55])

Distribution of reported cases: Italy [130] [55]**, Hungary** [46]**, Switzerland** [100]**, Poland** [117]

Ixodes frontalis

Overview: *Ixodes frontalis* has a pan-European distribution. However, it appears to be more frequent in warmer regions. It is an ornithophilic tick species that rarely feeds on other, exceptional hosts [124]. As such, it is commonly found on birds, mostly on Passeriformes, but the host range appears to be broad.

Passeriformes: 56; Charadriiformes: 1; Accipitriformes: 4; Galliformes: 4; Falconiformes: 1; Coraciiformes: 1; Gruiformes: 3; Columbiformes: 2; Strigiformes: 2

Hosts:

- Barn owl – *Tyto alba* (**F:** [91])
- Black redstart – *Phoenicurus ochruros* (**L:** [131]**; NA:** [101])
- Black-headed gull – *Chroicocephalus ridibundus* (**F:** [132])
- Bohemian waxwing – *Bombycilla garrulus* (**NA:** [101])
- Booted eagle – *Hieraaetus pennatus* (**A:** [127])
- Carrion crow – *Corvus corone* (**NA:** [133])
- Cetti's warbler – *Cettia cetti* (**L:** [87])
- Chicken – *Gallus gallus domesticus* (**NA:** [111])
- Coal tit – *Periparus ater*(**NA:** [96], [133])
- Common blackbird – *Turdus merula* (**L:** [82], [83], [86], [87], [100], [104], [112], [131], [132], [134], [135], [136], [137], [138] [139]; **N:** [82], [83], [87], [104], [108], [112], [127], [90], [131], [132], [134], [135], [136], [137], [138], [139], [140], [141], [23]; **M:** [136], [140]; **F:** [87], [91], [109], [131], [132], [134], [135], [136], [139], [142]; **A:** [143]; **NA:** [113], [133])
- Common buzzard – *Buteo buteo* (**N:** [127]; **A:** [127])

- Common chaffinch – *Fringilla coelebs* (**L:** [87], [90], [131], [134]; **N:** [82], [87], [134]; **F:** [86], [144], [87], [131], [135], [144]; **NA:** [96], [133])
- Common chiffchaff – *Phylloscopus collybita* (**L:** [23], [87], [131], [136]; **N:** [87], [145])
- Common firecrest – *Regulus ignicapilla* (**N:** [82], [87])
- Common kestrel – *Falco tinnunculus* (**F:** [139]; **NA:** [111] [133])
- Common kingfisher – *Alcedo atthis* (**F:** [132])
- Common linnet – *Carduelis cannabina* (**NA:** [96])
- Common moorhen – *Gallinula chloropus* (**F:** [146])
- Common nightingale – *Luscinia megarhynchos* (**N:** [136], [147]; **F:** [87])
- Common pheasant – *Phasianus colchicus* (**NA:** [133])
- Common redstart – *Phoenicurus phoenicurus* (**N:** [132], [145])
- Common reed bunting – *Emberiza schoeniclus* (**L:** [131])
- Common starling – *Sturnus vulgaris* (**NA:** [113], [133])
- Common whitethroat – *Sylvia communis*(**N:** [91], [119], [136], [140], [141], [145]; **F:** [91], [119])
- Common wood pigeon – *Columba palumbus* (**F:** [91]; **NA:** [133])
- Corn crake – *Crex crex* (**NA:** [133])
- Dunnock – *Prunella modularis* (**L:** [131]; **F:** [91], [119], [131])
- Eurasian blackcap – *Sylvia atricapilla* (**L:** [23], [87], [131], [134], [136]; **N:** [115], [87], [127], [46], [136], [145]; **F:** [91], [119], [136]; **A:** [112]; **NA:** [113])
- Eurasian blue tit – *Cyanistes caeruleus* (**L:** [82], [87], [91], [105], [119], [136]; **N:** [105]; **F:** [87], [105], [135], [136], [142]; **NA:** [133])
- Eurasian bullfinch – *Pyrrhula pyrrhula* (**F:** [91], [119])
- Eurasian collared dove – *Streptopelia decaocto* (**F:** [91], [132], [146], [148])
- Eurasian jay – *Garrulus glandarius* (**L:** [112]; **F:** [87]; **A:** [112]; **NA:** [96], [133])
- Eurasian magpie – *Pica pica* (**NA:** [133])
- Eurasian nuthatch – *Sitta europaea* (**NA:** [133])
- Eurasian reed warbler – *Acrocephalus scirpaceus* (**L:** [87], [132]; **N:** [87], [135], [145]; **F:** [87])
- Eurasian sparrowhawk – *Accipiter nisus* (**NA:** [133])
- Eurasian stonechat – *Saxicola torquatus* (**NA:** [133])
- Eurasian tree sparrow – *Passer montanus* (**F:** [91]; **NA:** [133])
- Eurasian treecreeper – *Certhia familiaris* (**NA:** [96])
- European goldfinch – *Carduelis carduelis* (**F:** [139])
- European greenfinch – *Carduelis chloris* (**L:** [82], [87], [132]; **F:** [23], [87], [46], [132]; **NA:** [133])

- European pied flycatcher – *Ficedula hypoleuca* (**NA:** [96])
- European robin – *Erithacus rubecula* (**L:** [82], [23], [83], [86], [87], [100], [104], [46], [131], [132], [134], [136], [137], [138]; **N:** [82], [83], [87], [100], [104], [106], [46], [131], [136], [137], [138], [149]; **M:** [87]; **F:** [23], [87], [91], [46], [138], [147])
- Fieldfare -*Turdus pilaris* (**F:** [139]; **NA:** [133])
- Goldcrest – *Regulus regulus* (**N:** [106]; **NA:** [96])
- Great grey shrike – *Lanius excubitor* (**NA:** [133])
- Great tit – *Parus major* (**L:** [82], [83], [87], [100], [105], [46], [131], [136]; **N:** [82], [83], [87], [105]; **F:** [87], [91], [105], [46]; **NA:** [133])
- Grey partridge – *Perdix perdix* (**NA:** [133])
- Grey wagtail – *Motacilla cinerea* (**N:** [132])
- Harris's hawk – *Parabuteo unicinctus* (**F:** [139])
- House sparrow – *Passer domesticus* (**L:** [90]; **N:** [91]; **F:** [87], [91], [90], [132]; **NA:** [133])
- Lesser redpoll – *Carduelis cabaret* (**F:** [91], [135])
- Long-eared owl – *Asio otus* (**L:** [132]; **N:** [150]; **F:** [150]; **NA:** [133])
- Long-tailed tit – *Aegithalos caudatus* (**N:** [87], [136]; **F:** [91], [119], [136], [137])
- Marsh tit – *Poecile palustris* (**NA:** [96])
- Melodious warbler – *Hippolais polyglotta* (**N:** [87])
- Mistle trush – *Turdus viscivorus* (**NA:** [113], [133])
- Red-legged partridge – *Alectoris rufa* (**M:** [132]; **A:** [151]; **NA:** [133], [152])
- Redwing – *Turdus iliacus* (**L:** [87], [135]; **N:** [87], [132], [135], [138]; **A:** [127]; **NA:** [96], [133])
- Ring ouzel – *Turdus torquatus* (**F:** [23]; **NA:** [96])
- Rook – *Corvus frugilegus* (**NA:** [96])
- Sardinian warbler – *Sylvia melanocephala* (**L:** [82]; **N:** [136]; **F:** [132])
- Scarlet-headed blackbird – *Amblyramphus holosericeus* (**F:** [91])
- Sedge warbler – *Acrocephalus schoenobaenus* (**F:** [87])
- Short-toed treecreeper – *Certhia brachydactyla* (**L:** [82], [87]; **N:** [82], [87]; **F:** [131])
- Song thrush – *Turdus philomelos* (**L:** [82], [23], [87], [106], [46], [131], [132], [135], [136], [137], [145]; **N:** [82], [23], [87], [100], [104], [106], [46], [131], [135], [136], [137], [138], [145]; **F:** [23], [87], [91], [109], [119], [135], [136], [142]; **NA:** [133])
- Subalpine warbler – *Sylvia cantillans* (**N:** [149])
- Tree pipit – *Anthus trivialis* (**NA:** [96])
- Water rail – *Rallus aquaticus* (**F:** [132]; **NA:** [96])
- Western yellow wagtail – *Motacilla flava* (**L:** [87]; **N:** [23])

- Whinchat – *Saxicola rubetra* (**N:** [149])
- Willow tit – *Poecile montana* (**NA:** [96]**,** [113])
- Willow warbler – *Phylloscopus trochilus* (**L:** [23], [90]**,** [138] [145]**; N:** [145]**; F:** [145])
- Winter wren – *Troglodytes troglodytes* (**L:** [82]**,** [83]**,** [87]**,** [131]**,** [132]**,** [138]**; N:** [82]**,** [83]**,** [87]**,** [97]**,** [131]**; F:** [91]**,** [119]**; NA:** [133])

Distribution of reported cases: United Kingdom [91] [96] [111] [119] [90] [140] [141] [142] [145]**, France** [132] [146] [148] [133]**, Spain** [109] [131] [136] [137] [151] [152]**, Poland** [104] [106]**, Greece** [86]**, Germany** [139]**, Netherlands** [108] [135]**, Norway** [115]**, Belgium** [105] [113]**, Hungary** [112] [46]**, Sweden** [122]**!** [138]**, Portugal (Azores)** [134]**, Italy** [88]**!** [143] [149]**, Switzerland** [144] [147]**, Moldova** [153]**!, Portugal** [82] [83] [87] [127] [150] **, Croatia** [101]**, Cyprus** [23]

Ixodes gibbosus

Overview: *Ixodes gibbosus* is a Mediterranean tick species, rarely reported from birds [7].

Passeriformes: 1

Hosts:

- Common blackbird – *Turdus merula* (**L/N:** [154]**)**

Distribution of reported cases: Greece [154]

Ixodes hexagonus

Overview: *Ixodes hexagonus* is a common parasite of European foxes and hedgehogs. [7] In the United Kingdom, this tick was reported from 5 passeriform, 1 galliform, 1 falconiform, 1 columbiform and, 1 strigiform birds. Whereas in Spain it was reported from 1 galliform bird. This tick species was also found on a bird in Germany but no information is available on the host species.

Passeriformes: 3; Galliformes: 2; Falconiformes: 1; Columbiformes: 1

Hosts:

- Chicken – *Gallus domesticus* (**F:** [91])
- Common kestrel- *Falco tinnunculus* (**NA:** [96])
- Common starling – *Sturnus vulgaris* (**NA:** [96])
- Common wood pigeon – *Columba palumbus* (**F:** [111])

- Eurasian blue tit- *Cyanistes caeruleus* (**NA:** [96])
- Red-legged partridge – *Alectoris rufa* (**NA:** [155])
- Winter wren – *Troglodytes troglodytes* (**NA:** [96])

Distribution of reported cases: United Kingdom [91] [96] [111], **Germany** [128]**!, Spain** [155]

Ixodes lividus

Overview: *Ixodes lividus* has a pan-European distribution, and it is the host-specific parasite of the sand martin (*Riparia riparia*). In Poland, it has been found on a Barn swallow (*Hirundo rustica*) as well.

Passeriformes: 2

Hosts:

- Barn swallow – *Hirundo rustica* (**NA:** [92])
- Sand martin – *Riparia riparia* (**L:** [97], [100], [119], [156]**in nest,** [157]**in nest,** [158], [159], [160]**in nest,** [161]; **N:** [146], [97], [100], [118], [119], [156]**in nest,** [157]**in nest,** [158], [159], [160]**in nest,** [161]; **M:** [97], [100], [156]**in nest,** [157]**in nest,** [160]**in nest,** [161]**in nest; F:** [97], [100], [113], [119], [156]**in nest,** [157]**in nest,** [160]**in nest,** [161]**in nest,** [162]; **A:** [159], [161]; **NA:** [91], [163], [164], [165], [166], [167])

Distribution of reported cases: United Kingdom [91] [119] [162] [163], **France** [146], **Portugal** [164], **Finland** [161], **Sweden** [97] [168]**!, Germany** [128]**!** [159], **Lithuania** [156] [157], **Moldova** [158], **Ukraine** [118], **Czech Republic** [160], **Schwitzerland** [100], **Hungary** [165] [166], **Poland** [92] [167], **Belgium** [113]

Ixodes persulcatus

Overview: *Ixodes persulcatus* is widely distributed in the Northern European region (Russia, Scandinavia, and the Baltic region) [7]**.** According to literature data however, it should be considered as a rare parasitee of birds in Europe. It was reported only from 2 passeriform bird species.

Passeriformes: 2

Hosts:

- Sedge warbler – *Acrocephalus schoenobaenus* (**N:** [169])

- Willow warbler – *Phylloscopus trochilus* (**N:** [97])

Distribution of reported cases: Estonia [169]**, Sweden** [97]

Ixodes ricinus

Overview: *Ixodes ricinus* has a pan-European distribution, including countries of Southern, Western, Central, Eastern and Northern Europe. As outlined below, this tick species was reported from 99 passeriform bird species, and from species of further 12 avian orders. According to available data, the immature stages of this tick species appear to be the most frequent hard ticks feeding on European birds.

Passeriformes: 99; Galliformes: 8; Accipitriformes: 6; Ciconiiformes: 1; Anseriformes: 3; Gruiformes: 3; Cuculiformes: 1; Charadriiformes: 7; Falconiformes: 1; Columbiformes: 2; Strigiformes: 3; Piciformes: 4; Bucerotiformes: 1

Hosts:

- Barn swallow – *Hirundo rustica* (**N:** [97])
- Barred warbler – *Sylvia nisoria* (**L:** [170]**; N:** [9], [170], [171]**; NA:** [112])
- Bearded reedling – *Panurus biarmicus* (**N:** [80])
- Black grouse – *Tetrao tetrix* (**L:** [172]**; N:** [97], [172])
- Black kite – *Milvus migrans* (**NA:** [112])
- Black redstart – *Phoenicurus ochruros* (**N:** [81], [106], [138], [144])
- Black stork – *Ciconia nigra* (**N:** [173])
- Bluethroat – *Luscinia svecica* (**L:** [97], [100], [108], [174]**; N:** [97], [135], [138], [170], [171], [175], [176], [177], [178])
- Blyth's reed warbler – *Acrocephalus dumetorum* (**N:** [169])
- Bohemian waxwing – *Bombycilla garrulus* (**NA:** [81]
- Brambling – *Fringilla montifringilla* (**L:** [100], [138], [144], [179]**; N:** [100], [9], [144], [179]**; NA:** [180])
- Canada goose – *Branta canadensis* (**L:** [172]**; N:** [172])
- Carrion crow – *Corvus corone* (**N:** [100]**; NA:** [96])
- Cetti's warbler – *Cettia cetti* (**L:** [82]**; N:** [82]**; NA:** [101])
- Chicken – *Gallus gallus domesticus* (**M:** [100])
- Coal tit – *Periparus ater* (**L:** [100], [181], [182]**; N:** [182], [183]**; NA:** [92], [95], [123], [180])
- Collared flycatcher – *Ficedula albicollis* (**N:** [184]**; NA:** [99])

- Common blackbird – *Turdus merula* (**L:** [115], [80], [81], [82], [83], [87], [94], [97], [100], [9], [104], [106], [108], [109], [117], [123], [46], [131], [135], [138], [139], [140], [141], [143], [144], [158], [170], [171], [174], [177], [178], [179], [181], [182], [184], [185], [186], [187], [188], [189], [190], [191], [192], [28], [193], [194], [195], [196], [197], [198], [199], [200], [201], [202], [203], [204]; **N:** [115], [80], [81], [82], [83], [87], [90], [91], [94], [97], [100], [9], [104], [106], [108], [109], [117], [118], [123], [46], [131], [135], [136], [137], [138], [139], [140], [141], [143], [144], [158], [169], [170], [171], [173], [174], [176], [177], [178], [179], [181], [182], [184], [185], [186], [187], [189], [190], [191], [192], [28], [193], [194], [195], [196], [197], [198], [199], [200], [201], [202], [203], [204], [205], [29]; **M:** [97]; **F:** [80], [81], [82], [87], [118], [138], [141]; **A:** [184]; **NA:** [95], [99], [101], [111], [113], [206], [207], [208])
- Common buzzard – *Buteo buteo* (**N:** [100]; **NA:** [92], [99], [101], [111], [112])
- Common chaffinch – *Fringilla coelebs* (**L:** [115], [81], [82], [83], [91], [100], [9], [104], [106], [108], [131], [135], [138], [141], [144], [158], [170], [174], [177], [178], [179], [181], [182], [185], [186], [189], [193], [197], [199], [200], [201], [202], [203], [204]; **N:** [115], [81], [82], [100], [104], [106], [108], [118], [135], [136], [138], [143], [144], [158], [170], [174], [177], [177][a], [178], [179], [181], [182], [185], [186], [191], [193], [197], [199], [200], [201], [202], [203], [204], [209]; **F:** [83], [87], [144]; **NA:** [99], [111], [112], [113] [123], [180], [188], [194], [207], [208], [210])
- Common chiffchaff – *Phylloscopus collybita* (**L:** [100], [104], [106], [46], [136], [177], [178], [193], [203], [29]; **N:** [80], [87], [94], [97], [104], [106], [46], [135], [138], [141], [145], [169], [174], [185], [28], [193], [197], [202], [204], [205]; **NA:** [123], [206]; **NA:** [126])
- Common coot – *Fulica atra* (**NA:** [92])
- Common crane – *Grus grus* (**NA:** [96])
- Common cuckoo – *Cuculus canorus* (**NA:** [92])
- Common firecrest – *Regulus ignicapilla* (**N:** [104]; **NA:** [188])
- Common grasshopper warbler – *Locustella naevia* (**L:** [187]; **N:** [104], [169], [187]; **NA:** [96])
- Common house martin – *Delichon urbicum* (**F:** [100]; **NA:** [96])
- Common kestrel- *Falco tinnunculus* (**L:** [100]; **N:** [100]; **NA:** [81])
- Common linnet – *Carduelis cannabina* (**L:** [141]; **N:** [108], [135], [170], [171], [174], [177], [178]; **NA:** [112])
- Common nightingale – *Luscinia megarhynchos* (**L:** [100], [108], [46], [143], [28], [204], [211]; **N:** [94], [100], [46], [136], [143], [28], [204], [211], [212]; **A:** [204]; **NA:** [81], [92], [99], [101])

- Common pheasant – *Phasianus colchicus* (**L:** [90], [97], [213]; **N:** [90], [97], [100], [108], [213]; **M:** [100]; **NA:** [81], [99], [111], [112])
- Common quail – *Coturnix coturnix* (**N:** [140])
- Common redpoll – *Carduelis flammea* (**L:** [170]; **N:** [138]; **NA:** [96])
- Common redstart – *Phoenicurus phoenicurus* (**L:** [115], [97], [9], [104], [106], [108], [135], [141], [144], [170], [171], [184], [189], [194], [196], [197], [203]; **N:** [115], [97], [9], [106], [108], [135], [138], [141], [144], [169], [170], [171], [175], [176], [177], [178], [184], [189], [194], [196], [197], [205]; **NA:** [99], [207])
- Common reed bunting – *Emberiza schoeniclus* (**L:** [80], [46], [170]; **N:** [94], [108], [135], [138], [169])
- Common rosefinch – *Carpodacus erythrinus* (**L:** [94]; **N:** [94], [169], [170], [174], [177], [178]; **NA:** [92])
- Common starling – *Sturnus vulgaris* (**L:** [81], [100], [9], [143], [170], [171], [174], [177], [178], [186], [197], [199], [201], [203]; **N:** [81], [100], [9], [138], [143], [170], [171], [177], [178], [186], [197], [199], [201], [203], [209]; **A:** [184]; **NA:** [96], [99], [112], [113], [210])
- Common whitethroat – *Sylvia communis* (**L:** [97], [9], [108], [90], [46], [135], [138], [140], [141], [170], [171], [174], [177], [178], [184], [187], [28], [196], [202]; **N:** [94], [97], [100], [9], [106], [108], [119], [46], [135], [138], [140], [141], [144], [145], [169], [170], [171], [174], [175], [177], [177][a], [178], [187], [189], [28], [196]; **F:** [97]; **NA:** [99], [207])
- Corn bunting – *Emberiza calandra* (**NA:** [99])
- Corn crake – *Crex crex* (**L:** [9]; **N:** [81], [9]; **NA:** [112])
- Dunnock – *Prunella modularis* (**L:** [115], [94], [104], [106], [108], [46], [135], [138], [141], [144], [170], [171], [174], [177], [178], [182], [185], [187], [28], [193], [197], [202], [29]; **N:** [115], [94], [97], [100], [9], [104], [106], [108], [46], [135], [138], [141], [144], [147], [170], [171], [174], [176], [177], [178], [182], [184], [185], [187], [28], [193], [196], [197], [202], [29]; **NA:** [123], [180], [208])
- Eurasian blackcap – *Sylvia atricapilla* (**L:** [82], [83], [97], [100], [9], [104], [106], [109], [46], [135], [136], [138], [143], [158], [170], [177], [178], [181], [182], [184], [185], [186], [187], [191], [28], [193], [195], [196], [197], [200], [202]; **N:** [82], [94], [97], [100], [104], [106], [109], [46], [135], [138], [140], [145], [158], [170], [174], [176], [177], [177][a], [178], [181], [183], [184], [187], [191], [28], [193], [195], [196], [197], [202], [29]; **A:** [183]; **NA:** [99], [123], [180], [188], [206])
- Eurasian blue tit- *Cyanistes caeruleus* (**L:** [80], [94], [100], [105], [170], [171], [181], [182], [185], [186], [193], [199], [201]; **N:** [94], [100], [104], [105], [108], [138], [169], [170], [171], [182], [185], [191], [197]; **NA:** [95], [99], [180], [188], [206], [208])

- Eurasian bullfinch – *Pyrrhula pyrrhula* (**L:** [100], [104], [170], [182]; **N:** [100], [9], [104], [170], [184], [195], [196], [202]; **NA:** [180], [206])
- Eurasian collared dove – *Streptopelia decaocto* (**NA:** [99])
- Eurasian curlew – *Numenius arquata* (**L:** [172], [214]; **N:** [172])
- Eurasian eagle-owl – *Bubo bubo* (**L:** [215]; **N:** [215], [216])
- Eurasian golden oriole – *Oriolus oriolus* (**L:** [99]; **N:** [99])
- Eurasian hoopoe – *Upupa epops* (**L:** [158]; **N:** [158], [173])
- Eurasian jay – *Garrulus glandarius* (**L:** [82], [100], [109], [158], [181], [182], [193], [197]; **N:** [81], [82], [99], [100], [108], [109], [135], [158], [181], [183], [193], [197]; **A:** [183]; **NA:** [92], [112], [180])
- Eurasian magpie – *Pica pica* (**L:** [81]; **N:** [81], [100]; **F:** [81], [100]; **NA:** [92], [96], [99], [101], [112])
- Eurasian nuthatch – *Sitta europaea* (**L:**[82], [94], [100], [104], [181], [186], [193], [201]; **N:** [100], [181], [186], [193], [197], [199]; **F:** [118]; **NA:** [99], [112], [113], [180], [188])
- Eurasian oystercatcher – *Haematopus ostralegus* (**L:** [97]; **N:** [97])
- Eurasian reed warbler – *Acrocephalus scirpaceus* (**L:** [87], [94], [97], [104], [46], [177][a], [28]; **N:** [87], [91], [94], [97], [100], [108], [119], [46], [135], [138], [143], [169], [170], [174], [177][a], [184], [28], [196], [29])
- Eurasian siskin – *Carduelis spinus*(**L:** [90], [100], [104], [182]; **N:** [100], [104], [135], [170], [182])
- Eurasian sparrowhawk – *Accipiter nisus* (**L:** [90]; **N:** [90], [97], [138], [170], [175], [204]; **A:** [204])
- Eurasian stonechat – *Saxicola torquatus* (**NA:** [96])
- Eurasian tree sparrow – *Passer montanus* (**L:** [100], [135], [185]; **N:** [100], [108], [135], [196]; **NA:** [92], [99], [112])
- Eurasian treecreeper – *Certhia familiaris* (**L:** [138], [182], [186], [187]; **N:** [144], [169] [170], [187], [194])
- Eurasian woodcock – *Scolopax rusticola* (**N:** [104]; **NA:** [99], [96])
- Eurasian wryneck – *Jynx torquilla* (**NA:** [99])
- European crested tit – *Lophophanes cristatus* (**L:** [106]; **N:** [106], [194])
- European golden plover – *Pluvialis apricaria* **(NA:** [217])
- European goldfinch – *Carduelis carduelis* (**N:** [174]; **NA:** [99], [123])
- European green woodpecker – *Picus viridis* (**N:** [197])
- European greenfinch – *Carduelis chloris* (**L:** [82] [83], [170], [171], [177], [178], [182]; **N:** [87], [99], [9], [104], [170], [171], [177], [178], [182], [185], [188], [29]; **NA:** [111], [113], [123])

- European herring gull – *Larus argentatus* (**N:** [108])
- European honey buzzard – *Pernis apivorus* (**NA:** [218])
- European pied flycatcher – *Ficedula hypoleuca* (**L:** [80], [87], [100], [9], [106]; **N:** [100], [9], [135], [184]; **NA:** [96], [113])
- European robin – *Erithacus rubecula* (**L:** [115], [80], [81], [82], [23], [83], [94], [97], [100], [9], [104], [106], [108], [109], [46], [131], [135], [136], [138], [140], [141], [143], [144], [158], [170], [171], [174], [177], [177][a], [178], [181], [182], [184], [185], [186], [187], [189], [191], [28], [193], [194], [195], [196], [197], [199], [200], [202], [203], [205], [29], [219]; **N:** [115], [80], [81], [82], [23], [83], [87], [94], [97], [100], [9], [104], [106], [108], [46], [131], [135], [136], [138], [143], [144], [147], [158], [169], [170], [171], [174], [175], [176], [177], [177][a], [178], [181], [182], [183], [184], [185], [186], [187], [189], [192], [28], [193], [194], [195], [196], [197], [199], [200], [202], [203], [204], [205], [29], [212]; **F:** [80], [104]; **A:** [183]; **NA:** [99], [113], [123], [138], [180], [188], [191], [206], [207], [208], [218])
- European serin – *Serinus serinus* (**L:** [144]; **N:** [83], [100], [144]; **NA:** [99])
- Fieldfare -*Turdus pilaris* (**L:** [81], [100], [140], [170], [177], [178]; **N:** [81], [97], [100], [9], [139], [140], [170], [177], [177][a], [178]; **NA:** [92], [112], [113], [123], [180])
- Garden warbler – *Sylvia borin* (**L:** [9], [179], [184]; **N:** [97], [100], [9], [135], [169], [170], [174], [177], [178], [179], [181], [184], [195]; **NA:** [92], [99])
- Goldcrest – *Regulus regulus* (**L:** [80], [97], [104], [106], [138]; **N:** [80], [97], [104], [106], [138], [169], [170], [184], [205]; **NA:** [208])
- Golden eagle – *Aquila chrysaetos* (**F:** [100])
- Great reed warbler – *Acrocephalus arundinaceus* (**N:** [169], [174], [177][a], [204], [29])
- Great spotted woodpecker – *Dendrocopos major* (**L:** [170], [171]; **N:** [170], [171]; **NA:** [99])
- Great tit – *Parus major* (**L:** [80], [81], [82], [83], [87], [94], [97], [100], [9], [104], [105] [106], [108], [116], [117], [46], [135], [141], [143], [144], [170], [171], [181], [182], [185], [187], [189], [191], [193], [194], [196], [197], [199], [200], [201], [203], [204]; **N:** [80], [81], [82], [83], [87], [91], [94], [100], [9], [104], [106], [105], [108], [116], [117], [118], [123], [46], [135], [138], [143], [144], [169], [170], [171], [177][a], [181], [182], [185], [187], [189], [191], [193], [195], [197], [199], [200], [201], [202], [203], [204], [205], [29], [209]; **M:** [118]; **F:** [118], [135]; **A:** [189]; **NA:** [95], [99], [180], [188], [206], [207], [208], [210], [220])
- Greenish warbler – *Phylloscopus trochiloides* (**L:** [184]; **N:** [9], [176])
- Grey partridge – *Perdix perdix* (**L:** [97]; **N:** [97], [173]; **NA:** [81], [112])
- Grey wagtail – *Motacilla cinerea* (**L:** [187]; **N:** [187], [123])

- Hawfinch – *Coccothraustes coccothraustes* (**L:** [99], [144], [186], [193], [199], [201], [203]; **N:** [94], [99], [100], [46], [135], [144], [174], [177], [178], [186], [28], [193], [199], [200], [201], [203], [204]; **A:** [204]; **NA:** [123])
- Hazel grouse – *Tetrastes bonasia* (**NA:** [112])
- Hooded crow – *Corvus cornix* (**NA:** [99], [112])
- House sparrow – *Passer domesticus* (**L:** [135], [191], [214]; **N:** [100], [135], [138]; **NA:** [99], [112], [188])
- Iberian chiffchaff – *Phylloscopus ibericus* (**L:** [82])
- Icterine warbler **–** *Hippolais icterina* (**L:** [138], [170], [177], [178], [184]; **N:** [100], [9], [135], [138], [177], [178], [196]; **NA:** [113])
- Lesser redpoll – *Carduelis cabaret* (**L:** [174]; **N:** [135], [177], [178])
- Lesser whitethroat – *Sylvia curruca* (**L:** [106], [138], [170], [171], [196]; **N:** [97], [9], [106], [135], [138], [170], [171], [175], [176], [177], [178], [196], [204])
- Long-eared owl – *Asio otus* (**N:** [100]; **NA:** [92], [96])
- Long-tailed tit – *Aegithalos caudatus* (**L:** [143])
- Mallard – *Anas platyrhynchos* (**NA:** [92])
- Marsh tit – *Poecile palustris* (**L:** [181], [185], [193]; **N:** [94], [9], [104], [181], [191], [193], [202]; **NA:** [95], [99])
- Marsh warbler – *Acrocephalus palustris* (**L:** [94], [97], [100], [196]; **N:** [94], [97], [100], [135], [138], [169], [170], [174], [177][a], [189], [195], [196], [204]; **NA:** [206], [207])
- Meadow pipit – *Anthus pratensis* (**L:** [94], [97], [141], [90], [172]; **N:** [97], [108], [90], [135], [140], [172], [177], [178]; **M:** [175]; **NA:** [113])
- Melodious warbler – *Hippolais polyglotta* (**L:** [136]; **N:** [143])
- Mew gull – *Larus canus* (**L:** [97]; **N:** [97], [214])
- Middle spotted woodpecker – *Dendrocoptes medius* (**NA:** [92], [99])
- Mistle trush – *Turdus viscivorus* (**L:** [135], [144], [188], [197]; **N:** [100], [144], [188], [197]; **NA:** [96], [99], [112])
- Northern goshawk – *Accipiter gentilis* (**N:** [173])
- Northern lapwing – *Vanellus vanellus* (**F:** [108]; **NA:** [96])
- Oriental turtle dove – *Streptopelia orientalis* (**N:** [118])
- Pechora pipit – *Anthus gustavi* (**NA:** [96])
- Pied wheatear – *Oenanthe pleschanka* (**NA:** [96])
- Red crossbill – *Loxia curvirostra* (**N:** [9]; **NA:** [96])
- Red kite – *Milvus milvus* (**N:** [100])
- Red-backed shrike – *Lanius collurio* (**L:** [170]; **N:** [138], [169], [170], [177][a], [193]; **NA:** [92], [99], [112])

- Redwing – *Turdus iliacus* (**L:** [97], [9], [106], [46], [135], [138], [144], [170], [171], [174], [189], [200], [205]; **N:** [97], [100], [9], [104], [106], [46], [135], [138], [141], [144], [169], [170], [171], [174], [176], [177], [178], [179], [189], [28], [200], [205], [29]; **NA:** [81], [113], [180], [207])
- Ring ouzel – *Turdus torquatus* (**N:** [100], [202]; **NA:** [96])
- River warbler – *Locustella fluviatilis* (**N:** [193])
- Rock bunting – *Emberiza cia* (**N:** [185])
- Rook – *Corvus frugilegus* (**L:** [121]; **N:** [118]; **M:** [118]; **F**: [118]; **NA:** [92],)
- Rustic bunting – *Emberiza rustica* (**NA:** [92])
- Sand martin – *Riparia riparia* (**L:** [160]**in nest; N:** [160]**in nest**)
- Sardinian warbler – *Sylvia melanocephala* (**L:** [82]; **N:** [87],)
- Savi's warbler – *Locustella luscinioides* (**L:** [46]; **N:** [46], [29])
- Sedge warbler – *Acrocephalus schoenobaenus* (**L:** [46], [28]; **N:** [94], [46], [135], [169], [175], [177][a], [28]; **NA:** [96])
- Short-toed treecreeper – *Certhia brachydactyla* (**L:** [82], [83], [100]; **N:** [82], [83])
- Skylark – *Alauda arvensis* (**L:** [170]; **N:** [99], [135], [144]; **NA:** [96])
- Song thrush – *Turdus philomelos* (**L:** [115], [80], [81], [82], [90], [97], [100], [9], [104], [106], [109], [123], [46], [135], [138], [141], [143], [144], [158], [170], [171], [174], [177], [179], [181], [182], [184], [185], [186], [187], [189], [191], [28], [194], [195], [197], [199], [200], [201], [202], [203], [205]; **N:** [115], [80], [81], [23], [87], [90], [97], [100], [9], [104], [106], [109], [123], [46], [135], [138], [140], [141], [143], [144], [158], [169], [170], [171], [173], [174], [176], [177], [178], [179], [181], [182], [184], [185], [186], [187], [189], [191], [28], [194], [195], [196], [197], [199], [200], [201], [202], [203], [205], [29], [209]; **NA:** [99], [101], [180], [206], [207], [210])
- Spotted flycatcher – *Muscicapa striata* (**L:** [175], [185], [196]; **N:** [97], [100], [175])
- Spotted nutcracker – *Nucifraga caryocatactes* (**N:** [144]; **NA:** [92])
- Tawny owl -*Strix aluco* (**NA:** [112])
- Thrush nightingale – *Luscinia luscinia* (**L:** [23], [97], [9], [106], [46], [138], [170], [171], [177][a], [184], [189], [28], [196], [202]; **N:** [97], [9], [106], [46], [138], [170], [171], [177][a], [184], [189], [28], [202], [204]; **A:** [204]; **NA:** [207])
- Tree pipit – *Anthus trivialis* (**L:** [87], [97], [100], [9], [106], [108], [138], [144], [170], [171], [175], [186], [28], [196], [200]; **N:** [97], [100], [9], [106], [108], [90], [138], [144], [169], [170], [171], [175], [186], [28], [196], [200], [203]; **NA:** [99], [101], [113])
- Turkey – *Meleagris gallopavo* – (**NA:** [81])
- Western jackdaw – *Corvus monedula* (**L:** [121]; **N:** [121]; **NA:** [99])
- Western yellow wagtail – *Motacilla flava* (**L:** [100], [9]; **N:** [97], [100], [175])
- Wheatear – *Oenanthe oenanthe* (**N:** [97], [141], [144], [177], [178]; **NA:** [126])

- Whinchat – *Saxicola rubetra* (**N:** [177], [178], [202]; **NA:** [96])
- White wagtail – *Motacilla alba* (**L:** [138]; **N:** [118], [90]; **M:** [118])
- Willow ptarmigan – *Lagopus lagopus* (**L:** [172], [221], [222]; **N:** [172], [221], [222])
- Willow tit – *Poecile montana* (**L:** [97], [104], [135], [185], [191]; **N:** [97], [100], [104], [135], [177][a], [185], [191], [194]; **NA:** [92], [123])
- Willow warbler – *Phylloscopus trochilus* (**L:** [115], [87], [97], [100], [9], [106], [108], [135], [138], [140], [144], [170], [171], [177], [178], [182], [184], [196], [202]; **N:** [115], [94], [97], [100], [9], [106], [108], [135], [138], [140], [143], [144], [145], [169], [170], [171], [175], [176], [177], [177][a], [178], [179], [90], [202]; **NA:** [99])
- Winter wren – *Troglodytes troglodytes* (**L:** [82], [83], [87], [97], [100], [104], [106], [109], [46], [131], [135], [138], [143], [144], [170], [171], [179], [181], [182], [187], [193], [196], [197], [203], [205], [29]; **N:** [82], [83], [87], [97], [100], [9], [104], [46], [131], [135], [138], [144], [169], [170], [171], [179], [181], [187], [188], [189], [193], [194], [197], [202], [203], [204], [205]; **F:** [91]; **NA:** [99], [123], [138], [180], [206], [207], [208])
- Wood warbler – *Phylloscopus sibilatrix* (**L:** [9], [106], [170], [171]; **N:** [9], [106]; **NA:** [99])
- Woodlark – *Lullula arborea* (**L:** [177], [178]; **N:** [144], [177], [178])
- Yellow-browed warbler – *Phylloscopus inornatus* (**NA:** [113])
- Yellowhammer – *Emberiza citrinella* (**L:** [99], [158]; **N:** [99], [104], [158], [193]; **NA:** [123], [81], [92],)

Distribution of reported cases: United Kingdom [91] [96] [111] [119] [90] [140] [141] [145] [172] [182] [213] [217] [221] [222], **Sweden** [97] [9] [122]**!** [138] [167]**!** [170] [171] [175] [184], **Slovakia** [99] [185] [191] [202], **Poland** [92] [104] [106] [117] [173] [186] [190] [199] [201], **Switzerland** [100] [144] [147] [180] [181] [183] [220], **Latvia** [194] [205], **Germany** [128]**!** [139] [189] [192] [195] [198] [206] [207], **Czech Republic** [94] [95] [123] [160]**!** [187] [193] [211] [212], **Belgium** [105] [113] [116] [215], **Italy** [88]**!** [143] [188] [200] [218] [219], **Netherlands** [108] [135] [214], **Estonia** [169], **Norway** [115] [174] [176] [177] [178], **Hungary** [112] [46] [28] [29], **Faroe Islands** [126], **Denmark** [196], **Romania** [80] [81] [89]**!** [121], **France** [197], **Moldova** [153]**!** [158], **Russia (Kaliningrad)** [179] [203] [210] [209], **Ukraine** [118], **Portugal** [82] [83] [87], **Spain** [109] [131] [136], **Lithuania** [177][a] [208], **Croatia** [101], **Bulgaria** [204] [216], **Cyprus** [23]

Ixodes rothschildi

Overview: *Ixodes rothschildi* has so far been reported from birds only in the United Kingdom and France. This tick species is a parasite of seabirds, collected from 4 charadriiform, 1 suliform, and 1 procellariform species.

Charadriiformes: 4; Suliformes: 1; Procellariiformes: 1

Hosts:

- Atlantic puffin – *Fratercula arctica* (**L:** [141], [223]; **N:**[141], [223]; **F:** [141]; **NA:** [84])
- Common murre – *Uria aalge* (**NA:** [96])
- European herring gull – *Larus argentatus* (**NA:** [96])
- European shag – *Phalacrocorax aristotelis* (**F:** [140])
- Manx shearwater – *Puffinus puffinus* (**NA:** [96])
- Razorbill – *Alca torda* (**N:** [224]; **F:** [224]**in burrows**)

Distribution of reported cases: United Kingdom [96] [140] [141] [223] [224]**, France** [84]

Ixodes unicavatus

Overview: *Ixodes unicavatus* is distributed in the coastal area of the UK, Sweden and France. The hosts are birds that usually nest on rocky cliffs. Six of such bird species have been described as hosts of this parasite.

Charadriiformes: 1; Suliformes: 3; Passeriformes: 2; Falconiformes: 1

Hosts:

- Atlantic puffin – *Fratercula arctica* (**NA:** [96])
- Common shag – *Gulosus aristotelis* (**NA:** [96])
- European rock pipit – *Anthus petrosus* (**NA:** [96])
- Great cormorant – *Phalacrocorax carbo* (**L:** [97]; **N:** [97]; **F:** [97]; **NA:** [96])
- Gyrfalcon – *Falco rusticolus* (**NA:** [96])
- Water pipit – *Anthus spinoletta* (**L:** [90])

Distribution of reported cases: United Kingdom [90] [96]**, Sweden** [97]**, France** [84]**!**

Ixodes uriae

Overview: *Ixodes uriae* is a common parasite of North European seabirds, as it was reported from 8 charadriiform, 1 anseriform, 3 suliform, and 1 procellariform bird species. According to the data it was also recorded from 2 passeriform bird species.

Charadriiformes: 8; Anseriformes: 1; Suliformes: 3; Procellariiformes: 1; Passeriformes: 3

Hosts:

- Atlantic puffin – *Fratercula arctica* (**N:** [90], [141], [225]**in nest; M:** [225]**in nest; F:** [90], [225]**in nest; NA:** [126] [226], [226][a], [226][b]; [227], [227][a], [227][b], [228], [228][a], [229])
- Black guillemot – *Cepphus grylle* (**NA:** [96])
- Black-legged kittiwake – *Rissa tridactyla* (**L:** [230]; **N:** [225]**in nest,** [230], [231], [232], [233]; **M:** [225]**in nest ,** [230]; **F:** [224], [225]**in nest,** [230], [232]; **NA:** [226][b], [227], [227][a], [227][b], [228], [228][a], [233], [234], [234][a], [234][b], [235], [236])
- Common eider – *Somateria mollissima* (**NA:** [237])
- Common murre – *Uria aalge* (**N:** [97], [225]**in nest,** [238], [239], [240]; **M:** [225]**in nest,** [238]; **F:** [97], [140], [224], [225]**in nest,** [238], [239], [240]; **NA:** [126], [226], [226][b], [227], [227][a] [227][b], [228], [228][a])
- Common starling – *Sturnus vulgaris* (**NA:** [96])
- Eurasian curlew – *Numenius arquata* (**NA:** [96])
- European herring gull – *Larus argentatus* (**N:** [233]**in nest; F:** [233]**in nest; NA:** [96])
- European shag – *Phalacrocorax aristotelis* (**N:** [141])
- Northern fulmar – *Fulmarus glacialis* (**NA:** [96])
- Northern gannet – *Morus bassanus* (**N:** [141]; **F:** [141])
- Razorbill – *Alca torda* (**N:** [240]; **F:** [240]; **NA:** [96], [226][b], [227][a], [227][b],)
- Red crossbill – *Loxia curvirostra* (**NA:** [96])
- Red-faced cormorant – *Urile urile* (**NA:** [226][b])
- Thick-billed murre – *Uria lomvia* (**N:** [238], [238][a]; **M:** [238], [238][a]; **F:** [238]; **NA:** [241], [242], [243])
- Wheatear – *Oenanthe oenanthe* (**NA:** [96])

Distribution of reported cases: United Kingdom [96] [141] [90] [224] [226] [227] [230] [231] [232] [234] [235] [239], **France** [233], [234][a], **Norway (Svalbard)** [238][a] [241] [242], **Norway** [225] [226][a] [227][a] [228] [234][b] [236] [240] [243], **Norway (Jan Mayen)** [238], **Iceland** [226][b] [227][b] [228] [237], **Faeroe Islands** [126] [229], **Sweden** [97]

Ixodes ventalloi

Overview: *Ixodes ventalloi*, commonly known as the rabbit tick as it mostly feeds on the European rabbit (*Oryctolagus cuniculus*), is a rare finding on birds [7]. This tick species has been recorded from 11 bird species. Four species belong to the order Strigiformes, which are often in contact with small mammals.

Strigiformes: 4; Passeriformes: 3; Galliformes: 3, Gruiformes: 1

Hosts:

- Barn owl – *Tyto alba* (**N:** [127])
- Black redstart – *Phoenicurus ochruros* (**N:** [149]**,** [244])
- Chukar partridge- *Alectoris chukar* (**NA:** [245])
- Common blackbird – *Turdus merula* **(N:** [149]**; F:** [87]**; NA:** [91])
- Common pheasant – *Phasianus colchicus* (**A:** [85])
- European robin – *Erithacus rubecula* (**N:** [244])
- Little owl – *Athene noctua* (**F**: [246])
- Long-eared owl – *Asio otus* (**N:** [141]**; F:** [141])
- Red-legged partridge – *Alectoris rufa* (**A:** [85]**; NA:** [155])
- Short-eared owl – *Asio flammeus* (**N:** [150]**; M:** [150]**; F:** [150])
- Water rail – *Rallus aquaticus* (**A:** [85])

Distribution of reported cases: Cyprus [245]**, Spain** [155] [246]**, Portugal** [87] [127] [150]**, Italy** [85] [149] [244]**, United Kingdom** [91] [141]

METASTRIATA

Amblyomma lepidum

Overview: While the immature stages of *Amlyomma lepidum* are relatively common bird parasites in Africa [124], this tick species has been reported only once in European territory, from a passeriform bird.

Passeriformes: 1

Hosts:

- Common blackbird – *Turdus merula* (**N:** [23])

Distribution of reported cases: Cyprus [23]

Amblyomma marmoreum

Overview: *Amblyomma marmoreum* is an African tick species, where it was reported from several bird species. [124] In Europe, it has been found on a Tree pipit in Italy.

Passeriformes: 1

Hosts:

- Tree pipit – *Anthus trivialis* **(N:** [149])

Distribution of reported cases: Italy [149]

Amblyomma nuttalli

Overview: *Amlyomma nuttali* is distributed in the Afrotropical region, where they may infest several bird species. [124] So far, we have only one report in Europe, where it was found on a Thrush nightingale (Passeriformes).

Passeriformes: 1

Hosts:

- Thrush nightingale – *Luscinia luscinia* (**N:** [23])

Distribution of reported cases: Cyprus [23]

Amblyomma variegatum

Overview: *Amblyomma variegatum* is an African tick species [124] and as such, it does not have European distribution. However, it was reported from 2 passeriform birds in Italy, and from one passeriform in Cyprus.

Passeriformes: 2

Hosts:

- Icterine warbler – *Hyppolais icterina* (**N:** [247])
- Tree pipit – *Anthus trivialis* **(N:** [23]**,** [244])

Distribution of reported cases: Italy [244] [247]**, Cyprus** [23]

Dermacentor reticulatus

Overview: *Dermacentor reticulatus* has a pan European distribution excepting Scandinavia [7], however its occurrence on birds is extremely rare. The only reports are from the United Kingdom and from Poland.

Passeriformes: 2

Hosts:

- European robin – *Erithacus rubecula* (**L:** [104])
- Meadow pipit – *Anthus pratensis* (**N:** [140])

Distribution of reported cases: Poland [104]**, United Kingdom** [140]

Dermacentor marginatus

Overview: *Dermacentor marginatus* is a common parasite throughout Europe, but not in Scandinavia [7]. Despite this fact, it is rare to find these ticks on birds**.** *D. marginatus* has been reported from 1 passeriform and 1 galliform bird species, as well as from the nest of a passeriform bird.

Passeriformes: 2; Galliformes: 1

Hosts:

- Bearded reedling – *Panurus biarmicus* (**L:** [248]**in nest; N:** [248]**in nest**)
- Turkey – *Meleagris gallopavo* – (**A:** [127])

- Yellowhammer – *Emberiza citrinella* (**NA:** [81]**,** [112])

Distribution of reported cases: Austria [248]**, Hungary** [112]**, Portugal** [127]**, Romania** [81]

Haemaphysalis concinna

Overview: *Haemaphysalis concinna* has a pan-European distribution. Interestingly, *H. concinna* seems to be extremely common on birds in Hungary, compared to other European countries. This parasite was reported from 36 different bird species so far. Thirty-three of these belong to the order Passeriformes.

Passeriformes: 33; Accipitriformes: 1; Galliformes: 1; Charadriiformes: 1

Hosts:

- Barred warbler – *Sylvia nisoria* (**NA:** [26])
- Black kite – *Milvus migrans* (**NA:** [112])
- Common blackbird – *Turdus merula* (**L:** [46]**; N:** [118]**,** [46]**,** [193]**,** [204]**; NA:** [99]**,** [26])
- Common chaffinch – *Fringilla coelebs* (**NA:** [99])
- Common grasshopper warbler – *Locustella naevia* (**L:** [46]**; N:** [46])
- Common nightingale – *Luscinia megarhynchos* (**L:** [46]**; N:** [46]**; NA:** [99]**,** [26])
- Common pheasant – *Phasianus colchicus* (**NA:** [99])
- Common reed bunting – *Emberiza schoeniclus* (**L:** [46]**; N:** [46])
- Common starling – *Sturnus vulgaris* (**NA:** [99])
- Dunnock – *Prunella modularis* (**L:** [46]**,** [28]**,** [193]**; N:** [46]**; NA:** [26])
- Eurasian blackcap – *Sylvia atricapilla* (**L:** [83]**,** [46]**,** [28]**; N:** [46]**,** [28]**; NA:** [26])
- Eurasian blue tit- *Cyanistes caeruleus* (**NA:** [99])
- Eurasian golden oriole – *Oriolus oriolus* (**N:** [99])
- Eurasian magpie – *Pica pica* (**NA:** [99])
- Eurasian nuthatch – *Sitta europaea* (**NA:** [99])
- Eurasian reed warbler – *Acrocephalus scirpaceus* (**L:** [46]**,** [28]**; N:** [46]**,** [28]**; NA:** [26])
- Eurasian tree sparrow – *Passer montanus* (**NA:** [99])
- Eurasian woodcock – *Scolopax rusticola* (**NA:** [99])
- European greenfinch – *Carduelis chloris* (**L:** [83]**; N:** [46]**; NA:** [26])
- European robin – *Erithacus rubecula* (**L:** [46]**,** [193]**; N:** [46]**,** [29]**; NA:** [99]**,** [26])
- Great reed warbler – *Acrocephalus arundinaceus* (**NA:** [26])

- Great tit – *Parus major* (**L:** [46]; **N:** [46], [118]; **NA:** [99], [26])
- Hawfinch – *Coccothraustes coccothraustes* (**L:** [46]; **N:** [46]; **NA:** [99], [26], [81])
- House sparrow – *Passer domesticus* (**NA:** [99])
- Lesser whitethroat – *Sylvia curruca* (**NA:** [26])
- Marsh warbler – *Acrocephalus palustris* (**L:** [46]; **N:** [46]; **NA:** [26])
- Red-backed shrike – *Lanius collurio* (**NA:** [99], [26])
- River warbler – *Locustella fluviatilis* (**N:** [193]; **NA:** [26])
- Rook – *Corvus frugilegus* (**L:** [121])
- Savi's warbler – *Locustella luscinioides* (**L:** [46], [28]; **N:** [46]; **NA:** [26])
- Sedge warbler – *Acrocephalus schoenobaenus* (**L:** [46]; **N:** [46]; **NA:** [26])
- Song thrush – *Turdus philomelos* (**L:** [46]; **N:** [46]; **NA:** [99], [26])
- Tree pipit – *Anthus trivialis* (**NA:** [99], [112]**]**
- Willow warbler – *Phylloscopus trochilus* (**L:** [23])
- Winter wren – *Troglodytes troglodytes* (**L:** [193])
- Yellowhammer – *Emberiza citrinella* (**L:** [99], [46], [193]; **N:** [99], [46], [193]; **NA:** [26])

Distribution of reported cases: Czech Republic [123]**!** [193], **Slovakia** [99], **Hungary** [112] [46] [28] [29] [26], **Romania** [89]**!** [121], **Ukraine** [118], **Bulgaria** [204], **Cyprus** [23]

Haemaphyalis erinacei

Overview: *Haemaphysalis erinacei*, (as its name suggests) is mainly a parasite of hedgehogs and small mammals [7]. Finding this tick on birds is a rare event. So far, it has been reported from the South-Eastern European region, where *H. erinacei* was found on on 4 different bird species. Interestingly, these 4 birds belonged to 4 different orders.

Caprimulgiformes: 1; Strigiformes: 1, Gruiformes: 1, Coraciiformes: 1

Hosts:

- Alpine swift – *Apus melba* (**N:** [249][a])
- Common Crane – *Grus grus* (**M:** [249])
- Eurasian eagle-owl – *Bubo bubo* (**F:** [216])
- European Bee-eater – *Merops apiaster* (**M:** [249])

Distribution of reported cases: **Bulgaria** [216], **Croatia** [249][a], **Bosnia and Herzegovina** [249]

Haemaphyalis parva

Overview: *Haemaphysalis parva* is a rare tick species on European birds. In Romania, it was found on 2 passeriforms, and on 1 galliform bird.

Passeriformes: 2; Galliformes: 1

Hosts:

- Common snipe – *Gallinago gallinago* (**NA:** [81])
- Rook – *Corvus frugilegus* (**L:** [121]; **N:** [121])
- Western jackdaw – *Corvus monedula* (**L:** [121])

Distribution of reported cases: **Romania** [81] [121]

Haemaphysalis punctata

Overview: *Haemaphysalis punctata* has a pan-European distribution, and its immature stages are fairly common parasites on birds, especially on Passeriformes.

Passeriformes: 40; Charadriiformes: 7; Falconiformes: 1; Strigiformes: 1; Galliformes: 2

Hosts:

- Black-headed gull – *Chroicocephalus ridibundus* (**F:** [97]; **NA:** [96])
- Cirl bunting – *Emberiza cirlus* (**L:** [87], [131], [136]; **N:** [87], [150])
- Common blackbird – *Turdus merula* (**L:** [82], [83], [87], [131], [136], [137]; **N**: [80], [82], [87], [131], [134], [136], [150], [250]; **NA:** [96], [99], [111], [112])
- Common chaffinch – *Fringilla coelebs* (**L:** [87], [131], [136]; **N:** [134], [136], [250])
- Common kestrel- *Falco tinnunculus* (**NA:** [96])
- Common linnet – *Carduelis cannabina* (**L:** [138])
- Common nightingale – *Luscinia megarhynchos* (**N:** [136])
- Common redstart – *Phoenicurus phoenicurus* (**L:** [214]; **F:** [97], [175]; **NA:** [92])
- Common reed bunting – *Emberiza schoeniclus* (**NA:** [96])
- Common starling – *Sturnus vulgaris* (**L:** [138]; **NA:** [96])
- Common tern – *Sterna hirundo* (**NA:** [96])
- Common whitethroat – *Sylvia communis* (**L:** [138]; **N:** [97]; **NA:** [96])
- Dunnock – *Prunella modularis* (**L:** [131]; **N:** [104], [131]; **NA:** [96])
- Eurasian blackcap – *Sylvia atricapilla* (**N:** [134])
- Eurasian blue tit – *Cyanistes caeruleus* (**L:** [138])

- Eurasian curlew – *Numenius arquata* (**N:** [214])
- Eurasian eagle-owl – *Bubo bubo* (**F:** [216])
- Eurasian jay – *Garrulus glandarius* (**L:** [82]**;** **NA:** [83]**,** [112])
- Eurasian magpie – *Pica pica* (**NA:** [112])
- Eurasian oystercatcher – *Haematopus ostralegus* (**L:** [97]**;** **N:** [97])
- Eurasian reed warbler – *Acrocephalus scirpaceus* (**N:** [150])
- Eurasian stonechat – *Saxicola torquatus* (**NA:** [96])
- Eurasian woodcock – *Scolopax rusticola* (**NA:** [99])
- European greenfinch – *Carduelis chloris* (**L:** [136])
- European herring gull – *Larus argentatus* (**NA:** [96])
- European robin – *Erithacus rubecula* (**L:** [87], [131], [219]**;** **N:**[131], [134]**;** **F:** [204]**;** **NA:** [96])
- European serin – *Serinus serinus* (**L:** [136])
- Great black-backed gull – *Larus marinus* (**NA:** [92])
- Great tit – *Parus major* (**L:** [87]**,** [131]; **N:** [250])
- Hooded crow – *Corvus cornix* (**NA:** [112])
- House sparrow – *Passer domesticus* (**L:** [136], [214]**;** **N:** [136], [214], [250]**;** **NA:** [96])
- Meadow pipit – *Anthus pratensis* (**L:** [214]**;** **NA:** [96])
- Melodious warbler – *Hippolais polyglotta* (**NA:** [96])
- Mistle trush – *Turdus viscivorus* (**NA:** [96])
- Red-billed chough – *Pyrrhocorax pyrrhocorax* (**NA:** [96])
- Red-legged partridge – *Alectoris rufa* (**NA:** [152])
- Ring ouzel – *Turdus torquatus* (**NA:** [112])
- Rook – *Corvus frugilegus* (**L:** [121], [250]; **N:** [121], [250]; **M:** [121]; **F:** [121]; **A**: [250])
- Skylark – *Alauda arvensis* (**NA:** [96])
- Song thrush – *Turdus philomelos* (**L:** [158]**;** **N:** [158]**,** [131]**;** **NA:** [96])
- Spotless starling – *Sturnus unicolor* (**L:** [136]**;** **N:** [136])
- Spotted flycatcher – *Muscicapa striata* (**L:** [23])
- Tree pipit – *Anthus trivialis* (**L:** [87])
- Turkey – *Meleagris gallopavo* – (**N:** [127]**;** **A:** [127]**;** **NA:** [81])
- Western jackdaw – *Corvus monedula* (**N:** [121]**;** **M:** [121]**;** **NA:** [96])
- Western yellow wagtail – *Motacilla flava* (**NA:** [101])
- Wheatear – *Oenanthe oenanthe* (**L:** [138]**;** **NA:** [96])
- Whinchat – *Saxicola rubetra* (**L:** [214])
- White wagtail – *Motacilla alba* (**L:** [138]**;** **N:** [97], [175]**;** **NA:** [96])
- Willow warbler – *Phylloscopus trochilus* (**L:** [23]**;** **NA:** [96])

- Yellowhammer – *Emberiza citrinella* (**NA:** [96]**,** [99])

Distribution of reported cases: Ukraine [250], **Spain** [131] [136] [152]**, Poland** [92] [104]**, United Kingdom** [96] [111]**, Slovakia** [99]**, Netherlands** [214]**, Sweden** [97] [138] [175], **Portugal (Azores)** [134]**, Moldova** [158]**, Portugal** [82] [83] [87] [127] [150]**, Romania** [81] [80] [121]**, Italy** [219]**, Hungary** [112]**, Croatia** [101]**, Bulgaria** [204] [216]**, Cyprus** [23]

Haemaphyalis sulcata

Overview: *Haemaphysalis sulcata* is a relatively rare parasite on birds. According to literature data, it has been recorded from 5 passeriform bird species so far.

Passeriformes: 5

Hosts:

- Common blackbird – *Turdus merula* (**N:** [204])
- Great reed warbler – *Acrocephalus arundinaceus* (**N:** [204])
- Savi's warbler – *Locustella luscinioides* (**N:** [204])
- Skylark – *Alauda arvensis* (**N:** [90])
- Thrush nightingale – *Luscinia luscinia* (**N:** [204])

Distribution of reported cases: United Kingdom [90], **Bulgaria** [204]

Hyalomma aegyptium

Hosts:

Overview: Although *Hyalomma aegyptium* is a common tick in the Mediterranean region, it is primarily a parasite of tortoises and humans [7]**.** Therefore, finding these ticks on European birds is an uncommon event. The only European report of this tick feeding on birds so far is from Greece, where this parasite has been reported from 2 passeriform species.

Passeriformes: 2

- Common blackbird – *Turdus merula* (**L:** [86])
- Common nightingale – *Luscinia megarhynchos* (**L:** [86])

Distribution of reported cases: Greece [86]

Hyalomma lusitanicum

Overview: *Hyalomma lusitanicum* is a common parasite of mammals in Spain and Portugal [7] [124]. Despite this fact, finding this tick species on bird is occasional. So far, it has been recorded from 2 galliform, 1 passeriform, 1 strigiform, 1 struthioniform and 1 columbiform birds from the Iberian Peninsula.

Passeriformes: 1; Galliformes: 2; Strigiformes: 1; Columbiformes: 1, Struthioniformes: 1

Hosts:

- Chicken **–** *Gallus gallus domesticus* (**N:** [251])

- Common blackbird – *Turdus merula* (**L:** [82]**; N** [82])
- Common ostrich – *Struthio camelus* (**A:** [127])
- Red-legged partridge – *Alectoris rufa* (**N:** [127]**; NA:** [152])
- Eurasian eagle-owl – *Bubo bubo* (**N:** [127])
- Common wood pigeon – *Columba palumbus* (**A:** [127])

Distribution of reported cases: Spain [152], **Portugal** [82] [127] [251]

Hyalomma marginatum (s.l.)

Overview: *Hyalomma marginatum* is a two-host tick species [124] that has a Palearctic distribution**.** While it is more common in the Mediterranean region, this parasite is also reported occasionally from Northern European countries. The most common bird hosts of *H. marginatum* are from the order Passeriformes

Passeriformes: 52; Accipitriformes: 5; Galliformes: 1; Strigiformes: 5; Falconiformes: 2; Coraciiformes: 1; Bucerotiformes: 1; Caprimulgiformes: 1, Columbiformes: 1

Hosts:

- Barn owl – *Tyto alba* (**L:** [150]; **N:** [150]**)**
- Barn swallow – *Hirundo rustica* (**N:** [150])
- Black kite – *Milvus migrans* (**N:** [150])
- Black redstart – *Phoenicurus ochruros* (**N:** [23])
- Bluethroat – *Luscinia svecica* (**N:** [252], [253]**; NA:** [253][b])
- Booted eagle – *Hieraaetus pennatus* (**N:** [127])
- Chicken – *Gallus gallus domesticus* (**NA:** [81])
- Collared flycatcher – *Ficedula albicollis* (**L:** [97])
- Common blackbird – *Turdus merula* (**L:** [82]**,** [136]**; N:** [23]**,** [136]**,** [150]**,** [254])
- Common buzzard – *Buteo buteo* (**N:** [127])
- Common chaffinch – *Fringilla coelebs* (**L:** [23], [136]**; N:** [23]**; F:** [138])
- Common chiffchaff – *Phylloscopus collybita* (**L:** [23])
- Common kestrel – *Falco tinnunculus* (**L:** [127]**; N:** [127]**; NA:** [253][d])
- Common kingfisher – *Alcedo atthis* (**N:** [150]**,** [127])
- Common nightingale – *Luscinia megarhynchos* (**L:** [136], [10][a]**; N:** [136], [204], [253][e], [10][a])
- Common redstart – *Phoenicurus phoenicurus* (**N:** [23]**,** [145]**,** [147]**,** [247] [252], [253][c]**; NA:** [96], [253][b], [253][d])
- Common whitethroat – *Sylvia communis* (**N:** [145]**,** [204]**,** [253][c]**,** [255]**; NA:** [96])
- Corn bunting – *Emberiza calandra* (**L:** [23])

- Crested lark – *Galerida cristata* (**L:** [23]; **N:** [23])
- Dunnock – *Prunella modularis* (**N:** [256])
- Eastern olivaceous warbler – *Iduna pallida* (**N:** [86])
- Eastern woodchat shrike – *Lanius senator niloticus* (**N:** [257])
- Eurasian blackcap – *Sylvia atricapilla* (**L:** [97]; **N:** [23], [253][c])
- Eurasian blue tit- *Cyanistes caeruleus* (**N:** [136], [150])
- Eurasian eagle-owl – *Bubo bubo* (**L:** [216]; **N:** [127], [150], [216]; **M:** [216])
- Eurasian hoopoe – *Upupa epops* (**NA:** [253][d])
- Eurasian jay – *Garrulus glandarius* (**N:** [82])
- Eurasian reed warbler – *Acrocephalus scirpaceus* (**L:** [10]; **N:** [127], [150]; **M:** [252]; **F:** [252], [10][a]; **NA:** [103])
- Eurasian scops owl – *Otus scops* (**L:** [23]; **N:** [23])
- Eurasian stonechat – *Saxicola torquatus* (**L:** [23]; **N:** [23], [127], [150])
- Eurasian tree sparrow – *Passer montanus* (**N:** [150])
- European greenfinch – *Carduelis chloris* (**L:** [23]; **N:** [23], [136], [150])
- European nightjar – *Caprimulgus europaeus* (**N:** [247])
- European pied flycatcher – *Ficedula hypoleuca* (**L:** [136])
- European robin – *Erithacus rubecula* (**L:** [138], [29]; **N:** [23], [147], [29], [253], [253][a], [256])
- European turtle dove – *Streptopelia turtur* (**L:** [23])
- Finsch's wheatear – *Oenanthe finschii* (**L:** [23]; **N:** [23])
- Great reed warbler – *Acrocephalus arundinaceus* (**L:** [23]; **N:** [10], [10][a])
- Great tit – *Parus major* (**L:** [136]; **N:** [136], [150])
- House sparrow – *Passer domesticus* (**L:** [136]; **N:** [136])
- Iberian grey shrike – *Lanius meridionalis* (**N:** [150])
- Lesser kestrel – *Falco naumanni* (**N:** [127])
- Lesser whitethroat – *Sylvia curruca* (**L:** [23])
- Little owl – *Athene noctua* (**N**: [150]; **NA:** [81])
- Marsh warbler – *Acrocephalus palustris* (**L:** [253][a]; **N:** [23], [204], [253][a], [253][c]; **NA:** [10][a])
- Mistle trush – *Turdus viscivorus* (**N:** [252], [254])
- Northern goshawk – *Accipiter gentilis* (**N:** [127])
- Ortolan bunting – *Emberiza hortulana* (**N:** [253][b])
- Red kite – *Milvus milvus* (**L:** [150])
- Rook – *Corvus frugilegus* (**N:** [254])
- Sardinian warbler – *Sylvia melanocephala* (**L:** [23]; **N:** [23])

- Savi's warbler – *Locustella luscinioides* (**N:** [10])
- Sedge warbler – *Acrocephalus schoenobaenus* (**N:** [97], [145], [10], [255], [257]; **F:** [10]; **NA:** [96], [167])
- Song thrush – *Turdus philomelos* (**L:** [23]; **N:** [23], [258])
- Spanish Sparrow – *Passer hispaniolensis* (**L:** [23])
- Spotted flycatcher – *Muscicapa striata* (**L:** [23]; **N:** [81])
- Tawny owl -*Strix aluco* (**N:** [127])
- Thrush nightingale – *Luscinia luscinia* (**L:** [23])
- Tree pipit – *Anthus trivialis* (**L:** [23]; **N:** [23], [9], [253], [253][b])
- Water pipit – *Anthus spinoletta* (**L:** [23])
- Western jackdaw – *Corvus monedula* (**N:** [121])
- Western olivaceous warbler – *Iduna opaca* (**N:** [255])
- Western yellow wagtail – *Motacilla flava* (**L:** [23], [257]; **N:** [23], [247]; **NA:** [167])
- Wheatear – *Oenanthe oenanthe* (**N:** [145]; **NA:** [96])
- Whinchat – *Saxicola rubetra* (**N:** [23]; **NA:** [96])
- White wagtail – *Motacilla alba* (**L:** [23]; **N:** [23], [97], [252])
- Willow warbler – *Phylloscopus trochilus* (**L:** [23], [255]; **N:** [138])
- Woodchat shrike – *Lanius senator* (**L:** [259]; **N:** [259])
- Yellowhammer – *Emberiza citrinella* (**NA:** [81])

Distribution of reported cases: Switzerland [147] [252], **Sweden** [97] [9] [122]**!** [138], **Slovakia** [253][a] [10], **Czech Republic** [253] [10][a] , **Italy** [247] [253][e] [260]**!**, **Greece** [86] [257] [259], **United Kingdom** [96] [145], **Hungary** [29], **Romania** [81] [121] [258], **Portugal** [82] [127] [150], **Spain** [136] [255], **France** [84]**!** [256], **Poland** [167], **Germany** [103] [253][c], **Finland** [253][b], **Slovenia** [253][d], **Ukraine** [254], **Bulgaria** [204] [216], **Cyprus** [23]

Hyalomma rufipes

Overview: *Hyalomma rufipes* is a two-host tick species [7]. It is a widely distributed, common bird parasite in the Mediterranean region. It isc occasionally reported on migrating birds from Northern European countries as well. Similarly to *H. marginatum* (in the past, *H rufipes* was considered as a subspecies of *H. marginatum* [124]) the most common bird hosts belong to Passeriformes.

Passeriformes: 46; Cuculiformes: 1; Piciformes: 1; Columbiformes: 1, Flaconiformes: 1, Bucerotiformes: 1, Strigiformes: 1

Hosts:

- Barred warbler – *Sylvia nisoria* (**N:** [23])
- Barn swallow – *Hirundo rustica* (**M:** [261])
- Black redstart – *Phoenicurus ochruros* (**N:** [244]**; NA:** [149])
- Black-eared Wheatear – *Oenanthe hispanica* (**L:** [23]**; N:** [23]
- Blue rock thrush – *Monticola solitarius* (**L:** [23])
- Crested lark – *Galerida cristata* (**L:** [23]**; N:** [23])
- Cyprus warbler – *Sylvia melanothorax* (**N:** [23])
- Collared flycatcher – *Ficedula albicollis* (**N:** [23], [244], [247]; **NA:** [149])
- Common blackbird – *Turdus merula* (**L:** [23]**; N:** [23])
- Common chaffinch – *Fringilla coelebs* (**N:** [23])
- Common chiffchaff – *Phylloscopus collybita* (**L:** [23])
- Common cuckoo – *Cuculus canorus* (**N:** [23], [247])
- Common kestrel- *Falco tinnunculus* (**L:** [23]**; N:** [23])
- Common nightingale – *Luscinia megarhynchos* (**L:** [247]**; N:** [23], [247]**,** [262])
- Common redstart – *Phoenicurus phoenicurus* (**L:** [23], [247]; **N:** [115], [23], [244], [247]; **NA:** [149])
- Common whitethroat – *Sylvia communis*(**L:** [247]; **N:** [115]**,** [23], [46], [244], [247]; **NA:** [149])
- Corn bunting – *Emberiza calandra* (**L:** [23])
- Cretzschmar’s bunting – *Emberiza caesia* (**L:** [23])
- Eastern olivaceous warbler – *Iduna pallida* (**L:** [23])
- Eastern subalpine warbler – *Sylvia cantillans* (**L:** [247])
- Eurasian blackcap – *Sylvia atricapilla* (**L:** [23]**; N:** [23], [256])
- Eurasian golden oriole – *Oriolus oriolus* (**N:** [244]**,** [247])
- Eurasian hoopoe – *Upupa epops* (**N:** [23])
- Eurasian reed warbler – *Acrocephalus scirpaceus* (**L:** [247]**; N:** [115])

- Eurasian scops owl – *Otus scops* (**L:** [23]; **N:** [23])
- Eurasian stonechat – *Saxicola torquatus* (**L:** [23]; **N:** [23])
- Eurasian wryneck – *Jynx torquilla* (**L:** [247])
- European goldfinch – *Carduelis carduelis* (**N:** [23])
- European greenfinch – *Carduelis chloris* (**N:** [23])
- European pied flycatcher – *Ficedula hypoleuca* (**L:** [247], **N:** [247])
- European robin – *Erithacus rubecula* (**N:** [23]; **NA:** [149])
- European turtle dove – *Streptopelia turtur* (**L:** [247])
- Garden warbler – *Sylvia borin* (**L:** [247]; **N:** [115])
- Great reed warbler – *Acrocephalus arundinaceus* (**L:** [247]; **N:** [247])
- Icterine warbler – *Hyppolais icterina* (**L:** [247]; **N:** [247])
- Isabelline wheatear – *Oenanthe isabellina* (**N:** [23])
- Lesser whitethroat – *Sylvia curruca* (**L:** [23]; **N:** [23])
- Pied wheatear – *Oenanthe pleschanka* (**L:** [23]; **N:** [23])
- Red-backed shrike – *Lanius collurio* (**L:** [23]; **N:** [23])
- Red-throated Pipit – *Anthus cervinus* (**L:** [23]; **N:** [23])
- Rock thrush – *Monticola saxatilis* (**L:** [23]; **N:** [23])
- Sedge warbler – *Acrocephalus schoenobaenus* (**N:** [247], [261]; **M:** [261]; **F:** [261])
- Song thrush – *Turdus philomelos* (**L:** [23]; **N:** [23]; **NA:** [149])
- Spotted flycatcher – *Muscicapa striata* (**L:** [247]; **NA:** [149])
- Thrush nightingale – *Luscinia luscinia* (**N:** [115])
- Tree pipit – *Anthus trivialis* (**L:** [23], [244]; **N:** [23], [247])
- Orphean Warbler – *Sylvia hortensis* (**L:** [23])
- Western yellow wagtail – *Motacilla flava* (**L:** [247], [253]**)**[f])
- Wheatear – *Oenanthe oenanthe* (**L:** [253][f], [23], **N:** [115], [23], [244], [247]; **NA:** [149])
- Whinchat – *Saxicola rubetra* (**L:** [247]; **N:** [244], [247], [263]; **NA:** [149])
- Willow warbler – *Phylloscopus trochilus* (**L:** [247]; **N:** [23])
- Wood warbler – *Phylloscopus sibilatrix* (**L:** [247]; **N:** [247]; **NA:** [149])

Distribution of reported cases: Norway [115], **Hungary** [46], **Italy** [149] [244] [247] [263] , **France (Corsica)** [261], **France** [256] [262], **Finland** [253][f], **Cyprus** [23]

Hyalomma truncatum

Overview: There is very limited information about *Hyalomma truncatum* as a bird parasite. According to the data, it has been found on a passeriform bird in Italy.

Passeriformes: 1

Hosts:

Whinchat – *Saxicola rubetra* (**L:** [247])

Distribution of reported cases: Italy [247]

Rhipicephalus annulatus

Overview: Despite the fact that *Rhipicephalus annulatus* is distributed in Southern-Europe [7] it is amazingly rare for this parasite to feed on birds. So far, only one such case was documented in Portugal.

Galliformes: 1

Hosts:

- Turkey – *Meleagris gallopavo* – (**N:** [127]**; A:** [127])

Distribution of reported cases: Portugal [127]

Rhipicephalus pusillus

Overview: *Rhipicephalus pusillus* is found in the Palaearctic region, mainly in Mediterranean climatic areas where birds are considered to be exceptional hosts [7]. So far, this was recorded only once.

Strigiformes: 1

Hosts:

- Eurasian eagle-owl – *Bubo bubo* (**A:** [127])

Distribution of reported cases: Portugal [127]

Rhipicephalus sanguineus

Overview: *Rhipicephalus sanguineus s.l.* is the most common tick species found on dogs in urban areas around the world [7]. However, finding them on birds is rare. So far, it has been recorded from a total of 6 bird species, belonging to 4 different orders.

Struthioniformes: 1; Strigiformes: 1; Passeriformes: 2; Accipitriformes: 2

Hosts:

- Common ostrich – *Struthio camelus* (**A:** [127]**; NA:** [96])
- Eurasian eagle-owl – *Bubo bubo* (**A:** [127])
- Great reed warbler – *Acrocephalus arundinaceus* (**F:** [81])
- House sparrow – *Passer domesticus* (**F:** [262] *Rhipicephalus sanguineus* sensu stricto (based on 99.7% 12S rRNA gene sequence identity between AY559843 and MH630345).
- Northern goshawk – *Accipiter gentilis* (**A:** [127])
- Short-toed snake eagle – *Circaetus gallicus* (**A:** [127])

Distribution of reported cases: Romania [81]**, France** [262]**, Portugal** [127]**, United Kingdom** [96]

Rhipicephalus turanicus

Overview: The taxonomic status of *Rhipicephalus turanicus* is still under discussion [7]. According to literature data, this tick species has been found on three bird species (all birds of prey) in Portugal and in Bulgaria. However, the Portuguese findings [150] were referred to in a later article by the same author [127] as *R. sanguineus.*

Accipitriformes: 2; Strigiformes: 1

Hosts:

- Common buzzard – *Buteo buteo* (**F:** [150]) (In a later article [127], the same author referred to this this finding as *R. sanguineus*)
- Eurasian eagle-owl – *Bubo bubo* (**M:** [216]**; F:** [216])
- Steppe eagle – *Aquila nipalensis* (**F:** [150]) (In a later article [127], the same author referred to this finding as *R. sanguineus*)

Distribution of reported cases: Portugal [150]**, Bulgaria** [216]

4.2 Long term evaluation of factors influencing the association of ixodid ticks with birds in Central Europe, Hungary

4.2.1 Identification of tick species and their occurrence on infested birds

During the study period 2395 tick-infested birds were captured, belonging to 51 different species, and a total of 5833 ticks were collected. The most frequent host species were the European Robin (*Erithacus rubecula*) ($n_{infested}$=521, $n_{captured}$=14809), followed by the Blackbird (*T. merula*) ($n_{infested}$=359, $n_{captured}$=1525). The mean number of ticks found on infested birds (i.e., intensity of infestation) was 2.44, while the median intensity was 1.

Based on morphological characteristics, eight tick species were identified, namely *Ixodes ricinus, Ixodes frontalis, Ixodes lividus, Ixodes festai, Ixodes arboricola, Haemaphysalis concinna, Haemaphysalis punctata* and *Dermacentor reticulatus* Table 2. Concerning molecular identification of *Hyalomma* species, one nymph showed 100% identity to sequences of *Hyalomma rufipes* reported in Africa and in Malta (cox1 gene: OQ540949 from Kenya; 12S rRNA gene: OL352890 from Malta, 16S rRNA gene: MK737649 from Egypt). Two further nymphs proved to be *Hyalomma marginatum*, one of them with 100% sequence identities to ticks reported from the eastern-middle-western Mediterranean region (cox1 gene: LC508365 from Portugal; 12S rRNA gene: OL352894 from Malta; 16S rRNA gene: KT391060 from Israel) and another with 99.8-100% sequence identities to specimens reported from the western Mediterranean region (cox1 gene: LC508365 from Portugal; 16S rRNA gene: LC508322 from Portugal).

Table 2. Ticks collected in Ócsa between March 2015 and November 2022.

Tick species	Larva	Nymph	Female	Male	Total
Ixodes ricinus	1229	2742	0	0	**3971**
Ixodes frontalis	52	38	12	0	**102**
Ixodes lividus	0	1	12	0	**13**
Ixodes festai	0	0	6	2	**8**
Ixodes arboricola	0	1	0	0	**1**
Haemaphysalis concinna	698	1008	0	0	**1706**
Haemaphysalis punctata	28	0	0	0	**28**
Dermacentor reticulatus	0	0	1	0	**1**
Hyalomma marginatum	0	2	0	0	**2**
Hyalomma rufipes	0	1	0	0	**1**

Altogether, 1872 (78.16%) of the captured, tick-infested birds carried *I. ricinus*, while 592 (24.72%) of them carried *H. concinna*. *Ixodes frontalis* was present on 51 birds (2.13%). The remaining seven tick species were carried by a combined total of 13 (0.54%) birds. One hundred thirty-one birds carried two tick species, and on one Song Thrush (*Turdus philomelos*) three different tick species were present simultaneously (*I. ricinus*, *I. frontalis* and *H. concinna*).

The 2395 tick-carrying birds captured during this study are summarized in Table 3 according to the characteristics that were examined. In the table, we also indicated how many bird species belonged to the given category. More detailed information can be found in Supplementary Table 3.

Table 3. Number of bird species according to their migration habit, habitat and feeding place.

Migration habit		Habitat		Feeding place	
R	78 (5 species)	Reed	621 (11 species)	Above ground	463 (23 species)
SDM	536 (12 species)	Forest	1356 (30 species)	Ground	1877 (23 species)
MDM	4 (1 species)	Meadow	47 (7 species)	Ground/Above ground	1 (4 species)
R/SDM	912 (10 species)	Forest/Meadow	367 (2 species)	Only flying insects	4 (1 species)
R/MDM	32 (2 species)	Sand walls	4 (1 species)		
LDM	833 (21 species)				

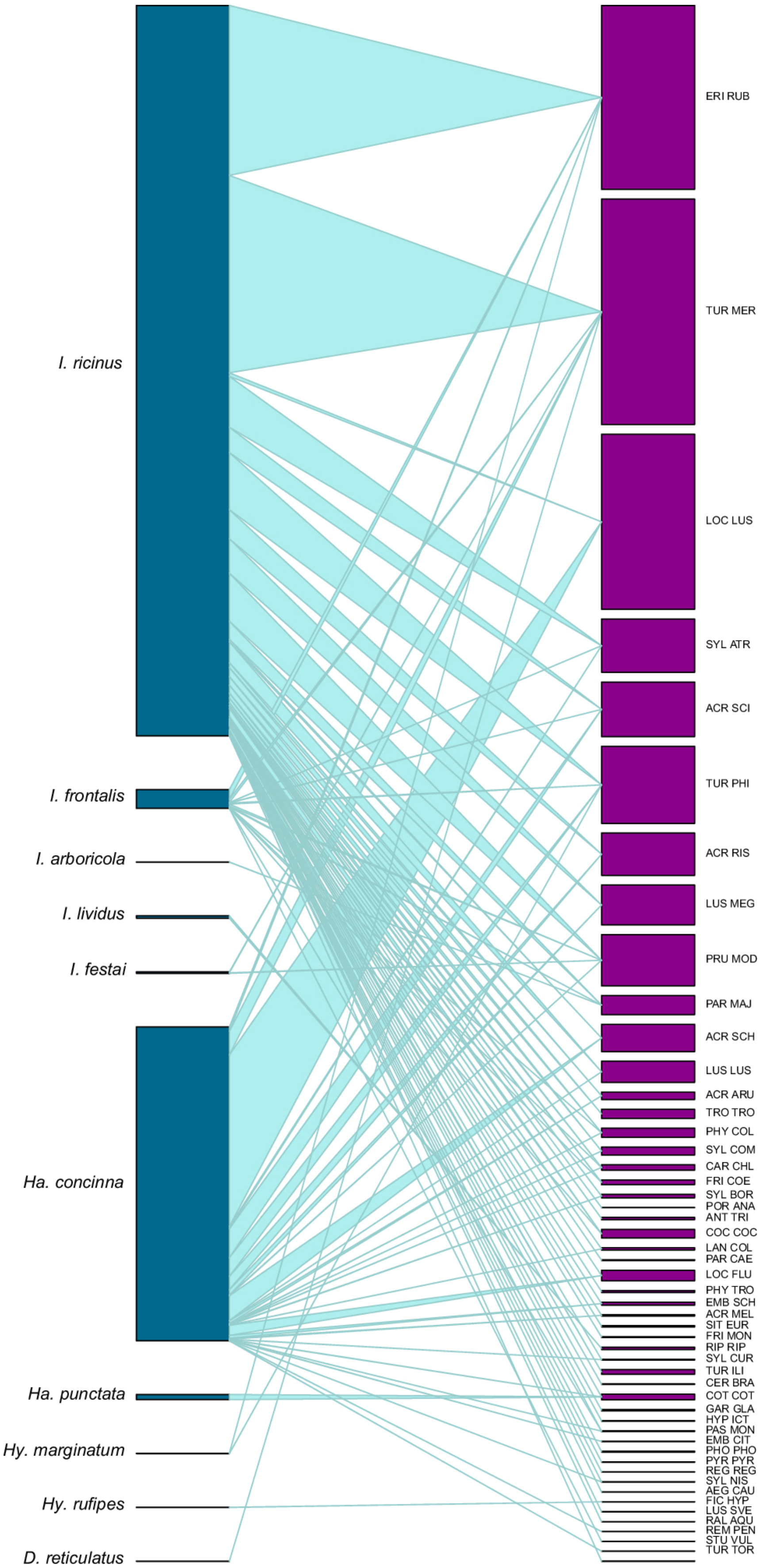
R: resident, SDM: short-distance migrants, MDM: middle-distance migrants, R/SDM: resident or short-distance migrants, R/MDM: residents or middle-distance migrants, LDM: long-distance migrants.

”Sand walls” and ”Only flying insects” are categories in which only the Sand Martin (*Riparia riparia*) belongs. On this bird, only *I. lividus* has been found.

4.2.2 Number and temporal occurrence of tick species, their host associations according to habitat and migration characteristics

All tick-host associations are visualized in Figure 1. Statistical analyses on ticks and their hosts according to their habitat and migration characteristics were only calculated for the most abundant tick species (*I. ricinus* and *H. concinna*), due to the fact that the limited numbers of other tick species precluded robust statistical analyses.

Figure 1. Tick-host associations visualized on a plotweb.



Ixodes ricinus (n_{total}=3971, n_{larvae}=1229, n_{nymphs}=2742)**:** *Ixodes ricinus* subadults occurred most frequently on resident and/or short-distance migrating birds with forest or forest and meadow habitat (Table 4 and Table 5), This category includes the two species on which the most ticks were found: Blackbirds (n_{ticks}=1073, n_{birds}=326), and European Robins (n_{ticks}=924, n_{birds}=490). (Table 6) *Ixodes ricinus* ticks were present on birds year-round, with nymphs reaching their peak in the first half of the sampling periods (1st of March – 30th of June), while larvae were the most abundant in the second half (1st of July – 31 of October). This was consistent over the course of eight years. The difference between the numbers of nymphs and larvae regarding their half-yearly activity was significant ($p<0.0001$) (Supplementary Figure 2)

Table 4. Number of ticks accoring to the habitat of their hosts.

Tick species and stage	**Meadow**	**Forest**	**Meadow/forest**	**Reed**
Ixodes ricinus L	22	981	105	121
Ixodes ricinus N	41	1482	981	238
Haemaphysalis concinna L	3	107	45	543
Haemaphysalis concinna N	6	128	84	790
Ixodes frontalis L	0	39	13	0
Ixodes frontalis N	0	32	4	2
Ixodes frontalis F	1	9	1	1
Ixodes festai F + M*[1]	0	3	5	0
Hyalomma marginatum N	0	2	0	0
Hyalomma rufipes N	0	1	0	0

L: larva, N: nymph, F: female, M: male.

*[1]: we treated males and females together, as the two males we found were in copulation with females.

Table 5. Number of ticks according to the migration habit of their hosts.

Tick species and stage	**R**	**SDM**	**MDM**	**R/SDM**	**R/MDM**	**LDM**
Ixodes ricinus L	16	278	1	586	3	345
Ixodes ricinus N	96	700	4	1450	70	422
Haemaphysalis concinna L	0	32	0	61	0	605
Haemaphysalis concinna N	1	95	0	109	2	801
Ixodes frontalis L	0	10	0	42	0	0
Ixodes frontalis N	2	7	0	26	1	2
Ixodes frontalis F	5	3	0	3	1	0
*Ixodes festai F + M**[1]	0	3	0	5	0	0
Hyalomma marginatum N	0	1	0	1	0	0
Hyalomma rufipes N	0	0	0	0	0	1

L: larva, N: nymph, F: female, M: male.

R: resident, SDM: short-distance migrants, MDM: middle-distance migrants, R/SDM: resident or short-distance migrants, R/MDM: residents ot middle-distance migrants, LDM: long-distance migrants.

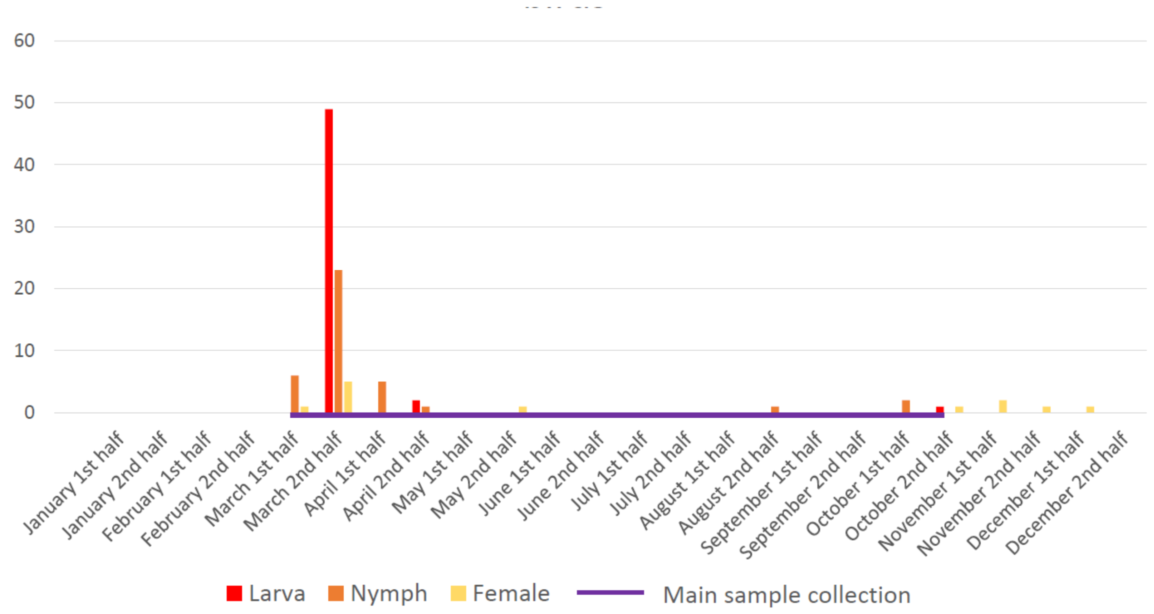
*[1]: we treated males and females together, as the two males we found were in copulation with females.

Table 6. The five most common hosts of *H. concinna* and *I. ricinus.*

(A)				
Bird species	**Number of tick-infested birds during our study**	**Total number of ticks**	**Number of *I. ricinus***	**Medians of total *I. ricinus* larva/nymph infestations**
TUR MER	359	1226	1073	1/2
ERI RUB	521	1000	924	1/1
TUR PHI	168	419	310	2/1
SYL ATR	199	290	277	1/1
PRU MOD	90	279	262	1/2
(B)				
Bird species	**Number of tick-infested birds during our study**	**Total number of ticks**	**Number of *H. concinna***	**Medians of total *H. concinna* larva/nymph infestations**
LOC LUS	243	952	933	2/2
ACR SCI	167	297	157	1/1
ACR SCH	54	148	135	2.5/1
TUR MER	359	1226	129	1/1
TUR PHI	168	419	102	1/1

Ixodes frontalis (n_{total}=102, n_{larvae}=52, n_{nymphs}=38, n_{female}=12)**:** The European Robin was the most common host of this tick species (n_{ticks}=52, n_{birds}=21). The second most frequently identified host species was the Blackbird (n_{ticks}=18, n_{birds}=4). *Ixodes frontalis* occurred most frequently on resident and/or short-distance migrating birds with forest habitat (Table 4 and Table *5*)**.** All stages of *I. frontalis* were the most abundant in the second half of March every year, during the eight-year-long study period (Figure 2**)**.

Figure 2. Total numbers of *Ixodes frontalis* ticks collected from birds.



Ixodes lividus (n_{total}=13, $n_{females}$=12, n_{nymphs}=1)***:*** All 13 *I. lividus* ticks were collected from four Sand Martins (*Riparia riparia*).

Ixodes festai (n_{total}=8, $n_{females}$=6, n_{males}=2)**:** In total eight ticks of this species were collected. Five ticks were removed from two Blackbirds and three ticks from two Dunnocks (*Prunella modularis*). It is important to mention, that the 2 males collected were not feeding, but were in copulation with females.

Ixodes arboricola (n_{total}=1, n_{nymphs}=1): Only one nymph was collected. It was removed from a Great Tit (*Parus major*).

Haemaphysalis concinna (n_{total}=1706, n_{larvae}=698, n_{nymphs}=1008): The majority (933 ticks, 54.7%) of individuals of this tick species were found on Savi's Warbler (*Locustella luscinioides*) (n_{birds}=238), making this bird the most common host of *H. concinna*. This tick species was also frequently collected from Eurasian Reed Warbler (*Acrocephalus scirpaceus*) (n_{ticks}=157, n_{birds}=82). The five most common hosts of *H. concinna* are listed in Table 6. Both *H. concinna* larvae and nymphs were active in the summer. However, the peaks of their abundance showed differences over the study period. In particular, the peak of infestation of birds with *H. concinna* larvae preceded that of its nymphs in 2015 and 2022, but the opposite trend was observed in 2017 and 2018. In other years, the peak larval and nymphal infestations occurred simultaneously (Supplementary Figure 2).

It was found that the host habitat (reed, forest, meadow, meadow/forest) of *I. ricinus* and *H. concinna* was significantly different ($p<0.0001$) (Table 4). We also compared the migratory habits (resident, short-distance migrants, middle-distance migrants, resident or short distance migrants, resident or middle-distance migrants, long-distance migrants) of the hosts of *I. ricinus* and *H. concinna*. The difference was strongly significant ($p<0.0001$) (Table 5). According to our findings, *H. concinna* occurred most frequently on long-distance migrant and reed-associated birds, while *I. ricinus* was the most abundant on short-distance migrants, with forest habitat (Table 4 and Table 5).

Haemaphysalis punctata ($n_{total}=28$, $n_{larvae}=28$)**:** A single Common Quail (*Coturnix coturnix*) was found with 28 feeding larvae.

Hyalomma marginatum ($n_{total}=2$, $n_{nymphs}=2$): One engorged nymph was collected from European Robin, and another from Song Trush (*T. philomelos*). Both were collected in the first half of April (in 2015, and 2016, respectively)

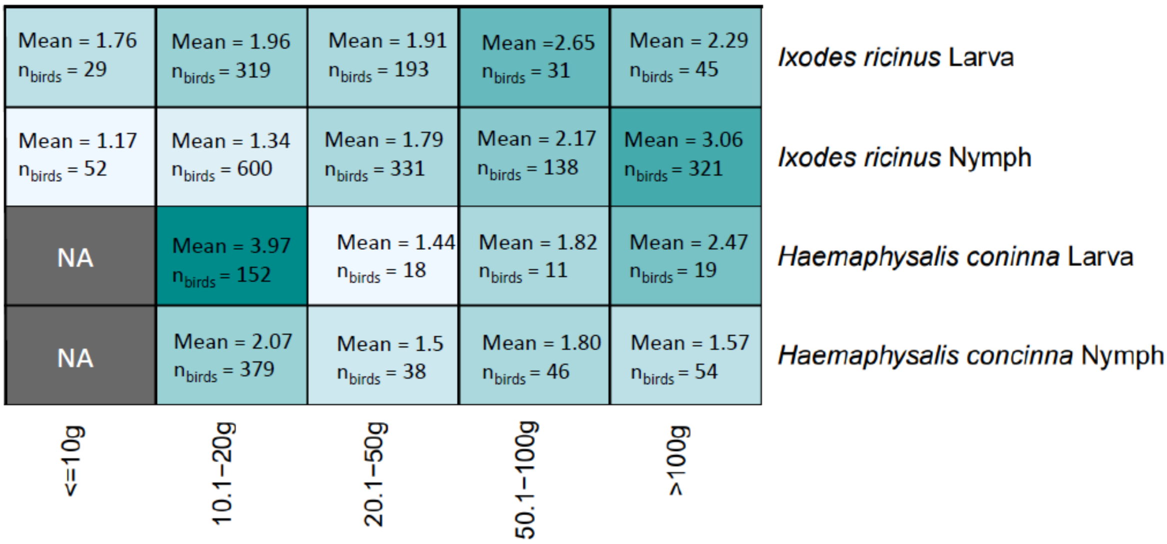
Hyalomma rufipes ($n_{total}=1$, $n_{nymph}=1$): Only one engorged nymph was found, which was feeding on a European Pied Flycatcher (*Ficedula hypoleuca*) in the second half of April 2015.

Dermacentor reticulatus ($n_{total}=1$, $n_{female}=1$): One female of this species was found on a Blackbird (*Turdus merula*), though it had not started to feed.

4.2.3 Host associations of ticks according to bird weight and feeding level characteristics

The mean intensity of infestation with *I. ricinus* nymphs was the highest among bird species with typical body weight above 100 grams, whereas this was the lowest among bird species measuring below 10 grams (Figure 3)The same was not true in the case of *H. concinna* nymphs, because the mean intensity of tick-infestation was the highest on birds weighing between 10.1 and 20 grams (Figure 3).

Figure 3. Mean tick intensity on birds, according to their average bodymass, visualized on a heatmap.



	<=10g	10.1–20g	20.1–50g	50.1–100g	>100g
Ixodes ricinus Larva	Mean = 1.76 n_{birds} = 29	Mean = 1.96 n_{birds} = 319	Mean = 1.91 n_{birds} = 193	Mean =2.65 n_{birds} = 31	Mean = 2.29 n_{birds} = 45
Ixodes ricinus Nymph	Mean = 1.17 n_{birds} = 52	Mean = 1.34 n_{birds} = 600	Mean = 1.79 n_{birds} = 331	Mean = 2.17 n_{birds} = 138	Mean = 3.06 n_{birds} = 321
Haemaphysalis coninna Larva	NA	Mean = 3.97 n_{birds} = 152	Mean = 1.44 n_{birds} = 18	Mean = 1.82 n_{birds} = 11	Mean = 2.47 n_{birds} = 19
Haemaphysalis concinna Nymph	NA	Mean = 2.07 n_{birds} = 379	Mean = 1.5 n_{birds} = 38	Mean = 1.80 n_{birds} = 46	Mean = 1.57 n_{birds} = 54

When the number of *I. ricinus*, *I. frontalis* and *H. concinna* infesting ticks were compared according to the feeding level of their hosts (only ground level or above ground categories were tested), *I. ricinus* tended to predominate on ground-feeding birds, whereas *H. concinna* nymphs and larvae were more often found on birds looking for food items above the ground level (p<0.0001). On the other hand, the difference was not significant between *I. ricinus* and *I. frontalis* (p=0.2584) (Table 7).

Table 7. Number of ticks according to the feeding places of their hosts.

Tick species and stage	**Ground**	**Above ground**	**Ground/above ground**
Ixodes ricinus L	896	328	5
Ixodes ricinus N	1836	890	16
Haemaphysalis concinna L	144	554	0
Haemaphysalis concinna N	204	804	0
Ixodes frontalis L	42	10	0
Ixodes frontalis N	31	7	0
Ixodes frontalis F	5	7	0
Ixodes festai F + M*1	5	3	0
Hyalomma marginatum N	2	0	0
Hyalomma rufipes N	0	1	0

L: larva, N: nymph, F: female, M: male.

*[1]: we treated males and females together, as the two males we found were in copulation with females.

4.3 Ornithological and molecular evidence of a reproducing *Hyalomma rufipes* population under continental climate in Europe

4.3.2 Host-associations of tick species and the migratory habits of their avian hosts

Associations of ticks collected in this study with different bird species are summarized in Supplementary Table 4. The Common Blackbird (*Turdus merula*) (n_{birds}=58, with 22.4% of total *I. ricinus* ticks) and the European Robin (*Erithacus rubecula*) (n_{birds}=105, with 32.4% of total *I. ricinus* ticks) were the two main hosts of *I. ricinus* in both the spring and the autumn tick collection periods. The preferred hosts of *I. frontalis* were also these two bird species (n_{birds}=4, with 22.2% of total *I. frontalis* ticks; and 5, with 38.9% of all *I. frontalis* ticks, respectively). *Haemaphysalis concinna* most often infested the Sedge Warbler (*Acrocephalus schoenobaenus*) (n_{birds}=49, with 17.1% of total *H. concinna* ticks) and Savi's Warbler (*Locustella luscinioides*) (n_{birds}=65, with 55,1% of all *H. concinna* ticks). *Hyalomma rufipes* was only collected on repeated occasions from Sedge Warblers (*A. schoenobaenus*) and Bearded Reedling (*Panurus biarmicus*), and once from a Common Whitethroat (*Curruca communis*) and from a European Pied Flycatcher (*Ficedula hypoleuca*). *Ixodes lividus* was only found once, on its specific host, the Sand Martin (*Riparia riparia*). Importantly, with the exception of the accidental finding of a single *D. reticulatus* female on a Common Blackbird, all other females (n=16) belonged to the two ornithophilic tick species *I. frontalis* (n=9) and *I. lividus* (n=6).

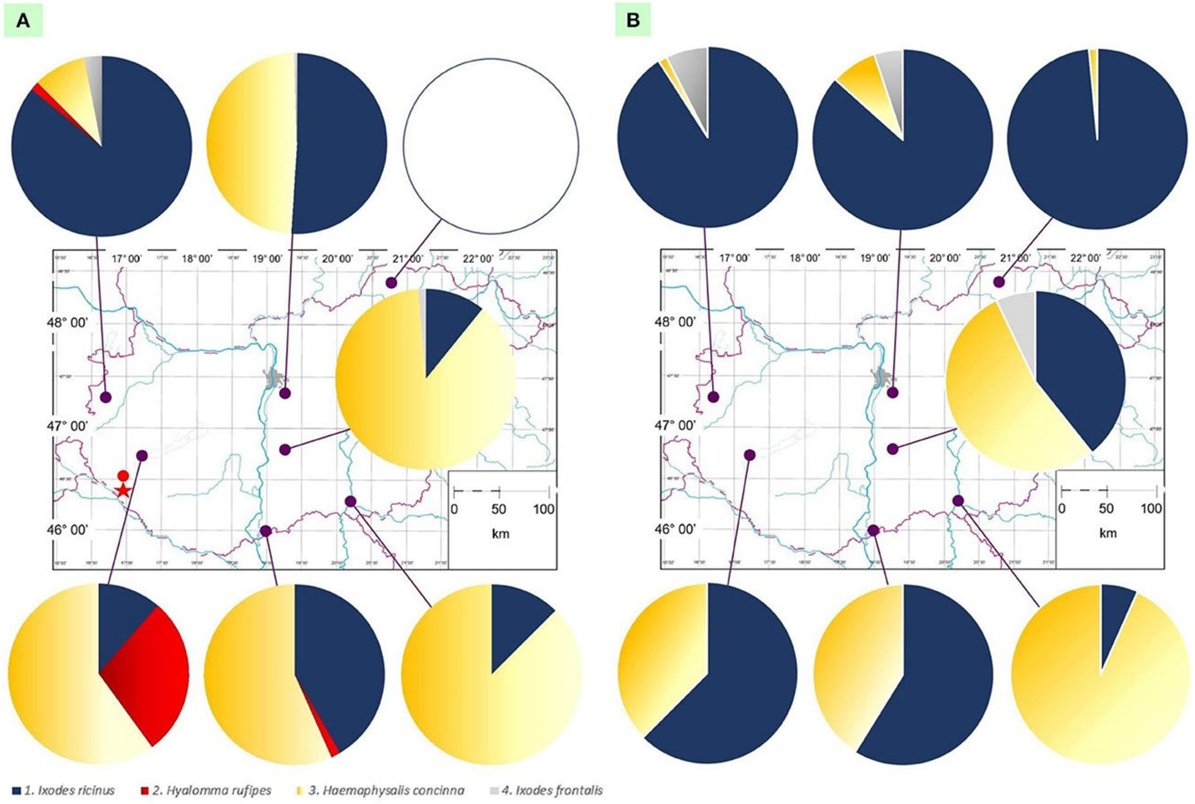
During the spring, at the ringing station in north-central Hungary (Ócsa) where the highest number of tick-infested birds were caught and which contributed the most balanced ratio of birds with different migratory habits to the study, there was a highly significant ($P < 0.0001$) difference between the host associations of *I. ricinus* and *H. concinna*, since the former predominated on resident and short-distance migrant bird species, but *H. concinna* on long-distance migrants. In the autumn, taking into account all ringing stations, the difference between these two tick species in the same comparison, and the association of *I. frontalis* with resident and short-distance migrant bird species was also highly significant ($P < 0.0001$).

4.3.3. Spatiotemporal occurrence of tick species

Ixodes ricinus and *H. concinna* were found to infest birds in both the spring and autumn collection periods (Figure 4) whereas the presence of *H. rufipes* was restricted to the first half of the year (Figure 4, Table 8-Table 9), and *I. frontalis* predominated in the autumn period

(Figure 4). Importantly, *H. rufipes* was collected from long-distance migrant birds in south and northwest Hungary in May and April, respectively (Table 9). However, all other specimens of this species were removed from birds in the middle of summer (late June) at one ringing station in the southwestern part of the country (Fenékpuszta).

Figure 4. Map of Hungary showing ringing stations and the ratio of tick species collected in (A) the first semiannual period (March to July) and (B) the second semiannual period (August to November). In the former (A) the location of the first Hyalomma nymph reported from a bird in Hungary in 1955 is marked with a red dot, and the place where adult *Hyalomma rufipes* ticks were found on cattle is indicated with a red star.



During the spring period, *I. ricinus* was the predominant tick species in the north, whereas *H. concinna* in central and south Hungary (Figure 4, Supplementary Table 5). However, in the autumn, *I. ricinus* represented the highest number of ticks from birds in north as well as in southwestern parts of the country, and *H. concinna* at two ringing stations, in central and southeast Hungary (Figure 4). *Hyalomma rufipes* was only found in the Transdanubian region and in one case along the southern reach of the Danube. On the other hand, *I. frontalis* could only be collected in northern and central locations during both spring and autumn and was absent from birds in southern parts of the country Figure 4).

Taken together, *I. ricinus* and *H. concinna* occurred on birds at all sampling sites, but their ratio was different according to these sites and semiannual periods. At the same time, the spatiotemporal distribution was limited in case of *H. rufipes* and *I. frontalis*.

4.3.4 Species and developmental stages of ticks infesting birds

During 2022, 539 individuals of 38 passeriform bird species were found to be tick-infested (approximately 39’000 bird were caught during the study period), from which altogether 956 ixodid ticks were collected (505 from March to July, and 451 from August to November: Table 8). The majority of developmental stages were nymphs (n=588), but 352 larvae and 16 females were also present. On most birds (n=381) only a single tick was found. The maximum number of ticks removed from a single bird was 30, and the mean intensity of tick-infestation was 1.78 tick/tick-infested bird in the whole study period.

Table 8. Total number of ticks collected in the first and second semiannual periods of 2022 at several locations of Hungary, according to their species and developmental state.

Tick species	Male	Female	Nymph	Larva	Total
Spring migration and summer nesting period (March–July)					
Ixodes ricinus	0	0	190	28	218
Haemaphysalis concinna	0	0	179	85	264
Hyalomma rufipes	0	0	11	1	12
Ixodes frontalis	0	2	1	1	4
Ixodes lividus	0	6	0	0	6
Dermacentor reticulatus	0	1	0	0	1
Autumn migration period (August–November)					
Ixodes ricinus	0	0	167	213	380

Haemaphysalis concinna	0	0	37	20	57
Hyalomma rufipes	0	0	0	0	0
Ixodes frontalis	0	7	3	4	14

Based on morphological characteristics, the ticks belonged to the following species: *Ixodes ricinus* (n=598), *Ixodes frontalis* (n=18), *Ixodes lividus* (n=6), *Haemaphysalis concinna* (n=321), and *D. reticulatus* (n=1). Morphologically, the twelve *Hyalomma* sp. ticks could only be identified on the genus level and so molecular identification was necessary. All *Hyalomma* nymphs were in a similar, advanced state of engorgement, but the single larva was flattened, appeared unengorged.

Based on the 16S rRNA gene, *Hyalomma* nymphs belonged to three haplotypes (Table 9). One of these collected in south Hungary (OQ103402) had 100% (383/383 bp) sequence identity to *H. rufipes* previously collected from a bird in north-central Hungary (Ócsa: KU170517) and another in Egypt (MK737650). The second haplotype (collected in northwest Hungary: OQ103403) differed in two, and the third haplotype (all other specimens: OQ103404-OQ103405) in one position of their 16S rRNA sequence, meaning 99.5% and 99.7% sequence identities to the above two reference sequences, respectively (Table 9). One haplotype (OQ108291) differed in one position, whereas all other *H. rufipes* specimens were 100% (645/645 bp) identical in the sequenced part of their *cox*1 gene (OQ108292-OQ108294) to a tick collected from a Eurasian Reed Warbler (*Acrocephalus scirpaceus*) in the Netherlands (MT757612) and another reported from Malta (OL339477). Interestingly, these *cox*1 sequences were more different (in two bps) from *H. rufipes* collected from a bird in a previous study in north-central Hungary (Ócsa: KU170491). In addition, all *H. rufipes* nymphs and the larva had identical 12S rRNA sequences (OQ103398-OQ103401), with 100% (341/341 bp) sequence identity to ticks collected from birds in Malta (OL352890) and in Italy (MW175439). Thus, the genus *Hyalomma* was exclusively represented by *H. rufipes* (n=12).

Table 9. Data of *Hyalomma* ticks collected in 2022 from birds at various ringing stations in Hungary.

Isolate code	**Bird species**	**Date**	**Region of Hungary (location)**	***Hyalomma* sp. (number, stage)**	**GenBank accession numbers according to the three genetic markers**		
					16S rRNA	**Cox1**	**12S rRNA**
BA2	SYL COM	May 14	South (Dávod)	H. rufipes (1xN)	OQ103402	OQ108291	OQ103398
GJ10	FIC HYP	April 23	Northwest (Tömörd)	H. rufipes (1xN)	OQ103403	OQ108292	OQ103399
BE02	ACR SCH	June 26	Southwest (Fenékpuszta)	H. rufipes (1xN)	OQ103404	OQ108293	OQ103400
BE03	ACR SCH	June 26	Southwest (Fenékpuszta)	H. rufipes (1xN)	OQ103404	OQ108293	OQ103400
BE04	ACR SCH	June 26	Southwest (Fenékpuszta)	H. rufipes (1xN)	OQ103404	OQ108293	OQ103400
BE05	PAN BIA	June 26	Southwest (Fenékpuszta)	H. rufipes (1xN)	OQ103405	OQ108294	OQ103401
BE06	PAN BIA	June 26	Southwest (Fenékpuszta)	H. rufipes (1xL, 5xN)	OQ103405	OQ108294	OQ103401

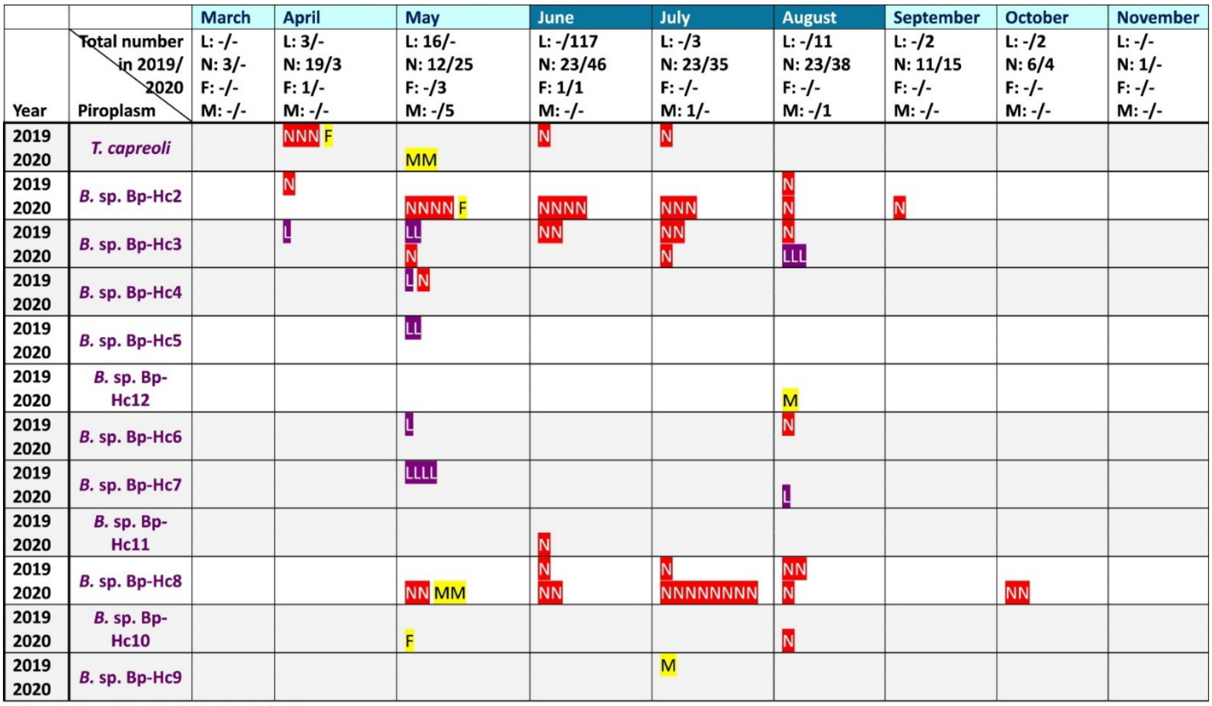
Identical background color in cells of the same column of a genetic marker indicates identical sequences.

4.4 Uneven temporal distribution of Far-Eastern piroplasms (Piroplasmida: Babesiidae, Theileriidae) in *Haemaphysalis concinna* in an urban biotope of the Western Palearctic focus region of this tick species

In both years of the study period, *H. concinna* questing activity was observed from March to November, but not during winter months. A total of 454 *H. concinna* individuals were collected, including 154 larvae, 287 nymphs, and 13 adults (seven males and six females). Nymphs and larvae reached their peak abundance in June, while the few adults predominated in May.

Eleven distinct *Babesia* genotypes and *T. capreoli* were identified in these ticks (Fig. 1). Regarding developmental stages, the *Babesia* prevalence was 9.7% (15/154) in larvae, 15.7%; (45/287) in nymphs, and 46%; (6/13) in adults. *Babesia* infection in *H. concinna* nymphs and adults was significantly more common in May (P=0.0173) and in July (P=0.0067) when compared to other months combined (Figure 5). Among *Babesia* genotypes, *Babesia* sp. Bp-Hc2 and *Babesia* sp. Bp-Hc8 were not detected in any *H. concinna* larvae, similarly to *T. capreoli*. On the contrary, *Babesia* sp. Bp-Hc5 and *Babesia* sp. Bp-Hc7 were only found in *H. concinna* larvae (Figure 5). Another genotype, *Babesia* sp. Bp-Hc3 was detected both in larvae and nymphs of *H. concinna* between April and August (Figure 5). *Theileria capreoli* was not detected in larvae, only in nymphs (n=5) males (n=2) and a female of *H. concinna*. All PCR-positive ticks occurred in the first five months of the sampling period (April to July). In addition, significantly (P = 0.0038) more *T. capreoli*-infected nymphs and adults were identified during the springtime (March-May) (6 infected, 71 uninfected) than in the summer and autumn combined (June-November) (2 infected, 229 uninfected).

Figure 5. Piroplasm species/genotypes according to the developmental stage or sex of Haemaphysalis concinna in which they were found in a certain month..

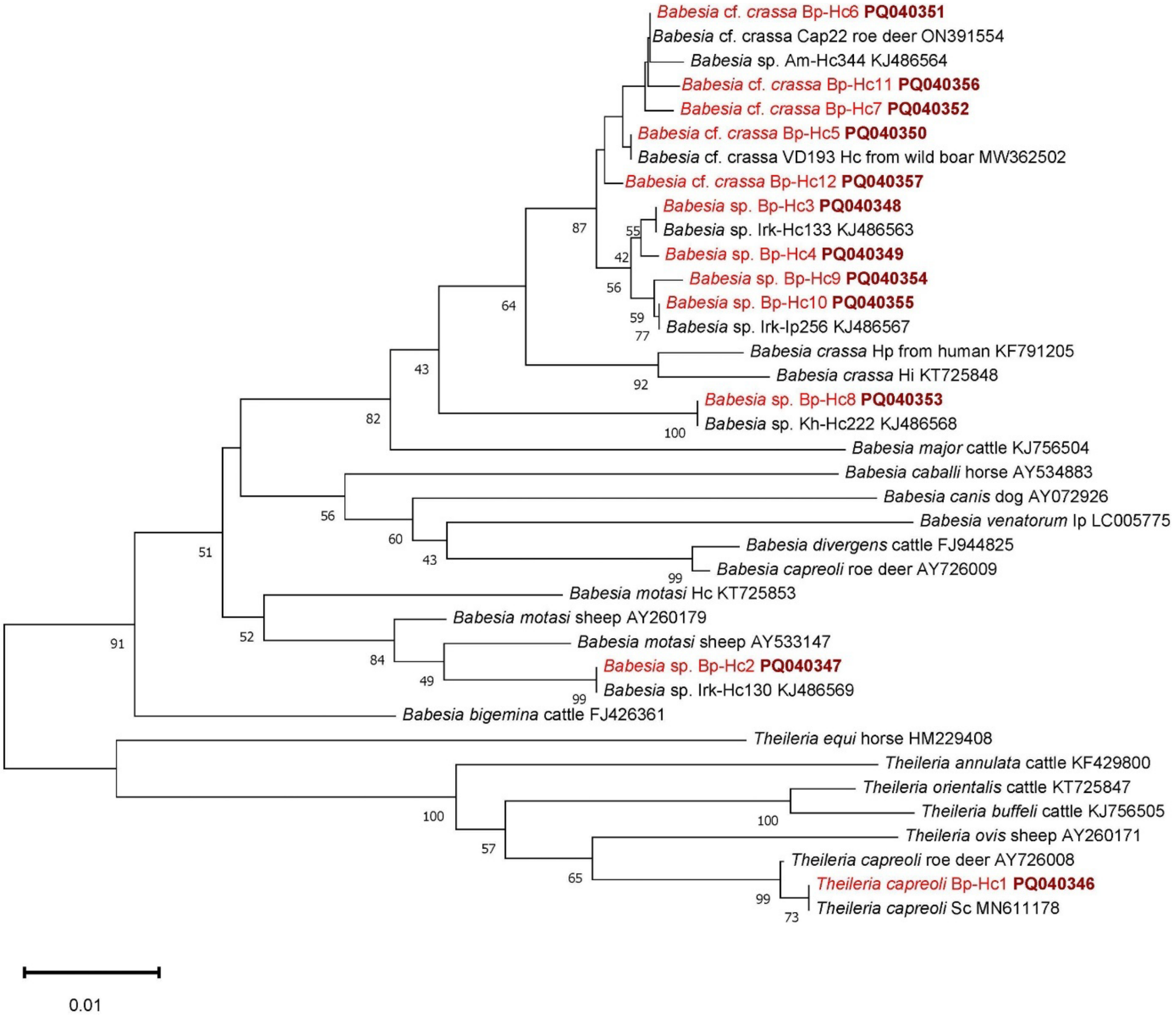


Year	Total number in 2019/ 2020 Piroplasm	March	April	May	June	July	August	September	October	November
		L: -/- N: 3/- F: -/- M: -/-	L: 3/- N: 19/3 F: 1/- M: -/-	L: 16/- N: 12/25 F: -/3 M: -/5	L: -/117 N: 23/46 F: 1/1 M: -/-	L: -/3 N: 23/35 F: -/- M: 1/-	L: -/11 N: 23/38 F: -/- M: -/1	L: -/2 N: 11/15 F: -/- M: -/-	L: -/2 N: 6/4 F: -/- M: -/-	L: -/- N: 1/- F: -/- M: -/-
2019	*T. capreoli*		NNN F		N	N				
2020				MM						
2019	*B.* sp. Bp-Hc2		N				N			
2020				NNNN F	NNNN	NNN	N	N		
2019	*B.* sp. Bp-Hc3		L	LL	NN	NN	N			
2020				N		N	LLL			
2019	*B.* sp. Bp-Hc4			L N						
2020										
2019	*B.* sp. Bp-Hc5			LL						
2020										
2019	*B.* sp. Bp-Hc12									
2020							M			
2019	*B.* sp. Bp-Hc6			L			N			
2020										
2019	*B.* sp. Bp-Hc7			LLLL						
2020							L			
2019	*B.* sp. Bp-Hc11									
2020					N					
2019	*B.* sp. Bp-Hc8				N	N	NN			
2020				NN MM	NN	NNNNNNNN	N		NN	
2019	*B.* sp. Bp-Hc10									
2020				F			N			
2019	*B.* sp. Bp-Hc9					M				
2020										

Abbreviations: *T – Theileria, B - Babesia*

Phylogenetically, *Babesia* genotypes identified in this study belong to the phylogenetic group of ruminant-associated species of Babesiidae which also include zoonotic species (Figure 6). These always clustered together with the corresponding, “Far Eastern” *Babesia* genotypes, with low to moderate support. Importantly, two of these *Babesia* variants were only represented by a single genotype and were never detected in larvae during this study (Figure 6).

Figure 6. Phylogenetic tree of Babesiidae and Theileriidae based on the 18S rRNA gene, made with the Neighbor-Joining method and p-distance model. In each row, after the species or genus name, the host (if known) and the GenBank accession number are shown. Sequences obtained in this study are in red and bold accession numbers. The analysis involved 38 nucleotide sequences. There were 445 positions in the final dataset. The scale-bar indicates the number of substitutions per site.



4.5 Contributions to our knowledge on avian louse flies (Hippoboscidae: Ornithomyinae) with the first European record of the African species *Ornithoctona laticornis*

4.5.1 Species and numbers of louse flies

During the eight-year-long sample collection period, 237 louse flies were collected from 175 birds (n_{flies}=219) of 32 species, and from the environment of the ringing facilities (n_{flies}=18) at multiple locations of Hungary. The mean intensity of infestation was 1.13, and the median intensity of infestation was 1. According to the morphological identification, the louse flies found belonged to six species: *Ornithomya avicularia (*n=168*)*, *Ornithomya biloba* (n=23), *Ornithomya fringillina* (n=17), *Ornithomya chloropus* (n=3), *Ornithoica turdi* (n=24) and *Ornithoctona laticornis* (n=1)*.* The parasite-host associations are visualized in Figure 7 and listed in Table 10.

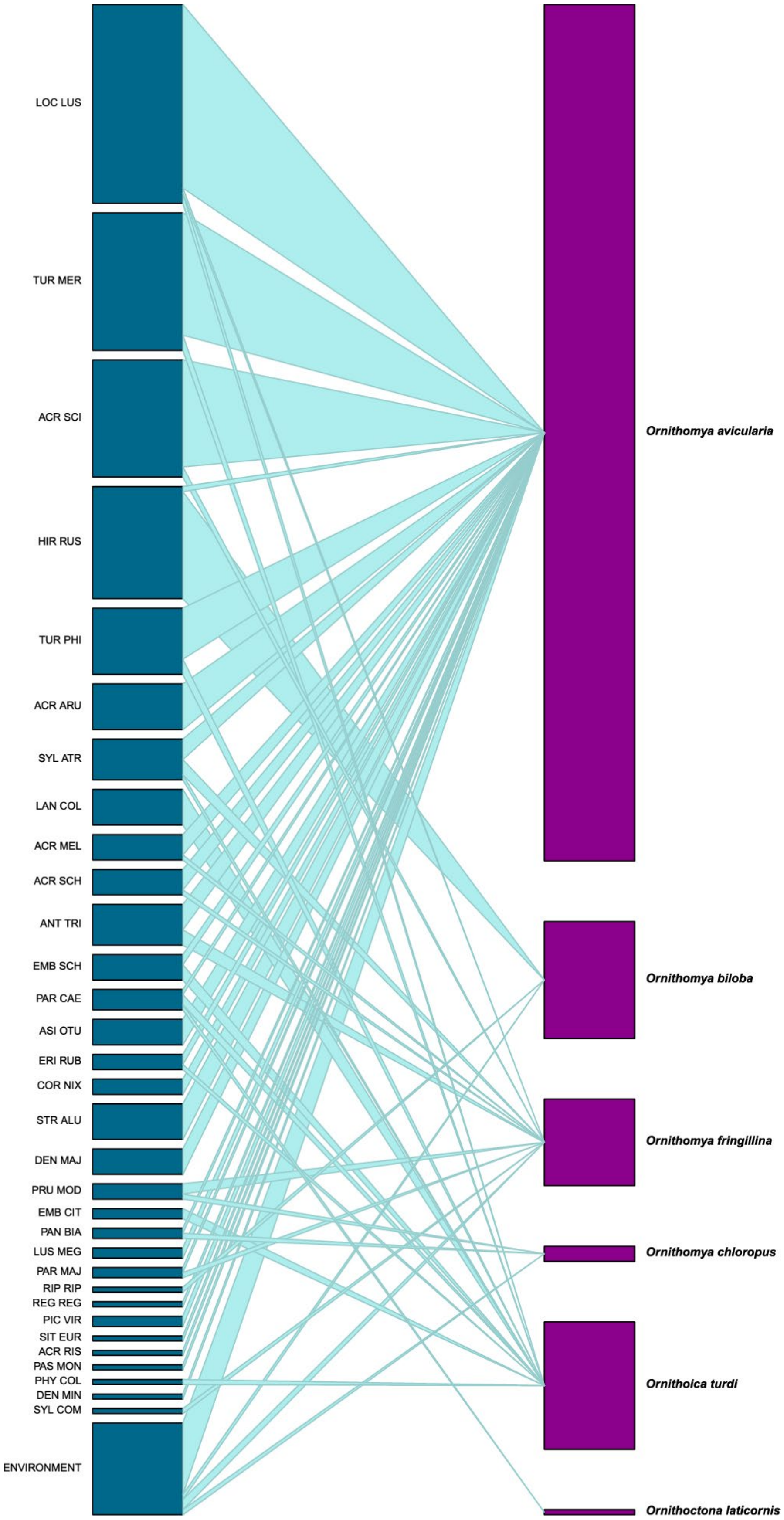
Table 10. Total number of ornithophilic louse fly species collected according to the host species.

HURING code for bird species	**Total number of infested birds**	**Louse fly species identified (n)**					
		Ornithomya avicularia	***Onrnithomya biloba***	***Ornithomya fringillina***	***Ornithomya chloropus***	***Ornithoica turdi***	***Ornithoctona laticornis***
LOC LUS	32	36	–	1	–	2	–
TUR MER	25	24	–	–	–	3	–
ACR SCI	23	21	–	2	–	–	–
HIR RUS	21	1	21	–	–	–	–
TUR PHI	11	10	–	–	–	3	–
ACR ARU	9	9	–	–	–	–	–
SYL ATR	8	4	–	3	–	1	–
LAN COL	5	–	–	–	–	7	–

HURING code for bird species	**Total number of infested birds**	**Louse fly species identified (n)**					
		Ornithomya avicularia	***Onrnithomya biloba***	***Ornithomya fringillina***	***Ornithomya chloropus***	***Ornithoica turdi***	***Ornithoctona laticornis***
ACR MEL	5	4	–	1	–	–	–
ACR SCH	5	4	–	1	–	–	–
ANT TRI	5	5	–	3	–	–	–
EMB SCH	4	2	–	–	–	3	–
PAR CAE	4	1	–	–	–	2	1
ASI OTU	4	5	–	–	–	–	–
ERI RUB	3	2	–	–	–	1	–
COR NIX	3	3	–	–	–	–	–
STR ALU	3	7	–	–	–	–	–
DEN MAJ	3	5	–	–	–	–	–
PRU MOD	3	–	–	2	1	–	–
EMB CIT	2	–	–	–	–	2	–
PAN BIA	2	1	–	–	1	–	–
LUS MEG	2	2	–	–	–	–	–
PAR MAJ	2	1	–	1	–	–	–

HURING code for bird species	**Total number of infested birds**	**Louse fly species identified (n)**					
		Ornithomya avicularia	***Onrnithomya biloba***	***Ornithomya fringillina***	***Ornithomya chloropus***	***Ornithoica turdi***	***Ornithoctona laticornis***
RIP RIP	1	–	1	–	–	–	–
REG REG	1	1	–	–	–	–	–
PIC VIR	1	2	–	–	–	–	–
SIT EUR	1	1	–	–	–	–	–
ACR RIS	1	1	–	–	–	–	–
PAS MON	1	1	–	–	–	–	–
PHY COL	1	–	–	–	–	1	–
DEN MIN	1	1	–	–	–	–	–
SYL COM	1	–	–	1	–	–	–
Not applicable	18	14	1	2	1	–	–
Total	193	168	23	17	3	25	1

Figure 7. Louse fly–host associations found during the study, visualized on a plotweb.



The maximum number of different louse fly species infesting the same bird was two. This only happened in the case of two birds: a Song Thrush (*Turdus philomelos*) and a Common Reed Bunting (*Emberiza schoeniclus*). On these birds, the co-infestation of *O. avicularia* and *O. turdi* was detected (one-one specimens).

Ornithoctona laticornis (n=1). Only one specimen of this species was found. It was removed from a Eurasian Blue Tit (*Cyanistes caeruleus*). (Table 10, Figure 8, Figure 9).

Figure 8. Dorsal (A) and ventral (B) pictures of the louse fly *Ornithoctona laticornis.*

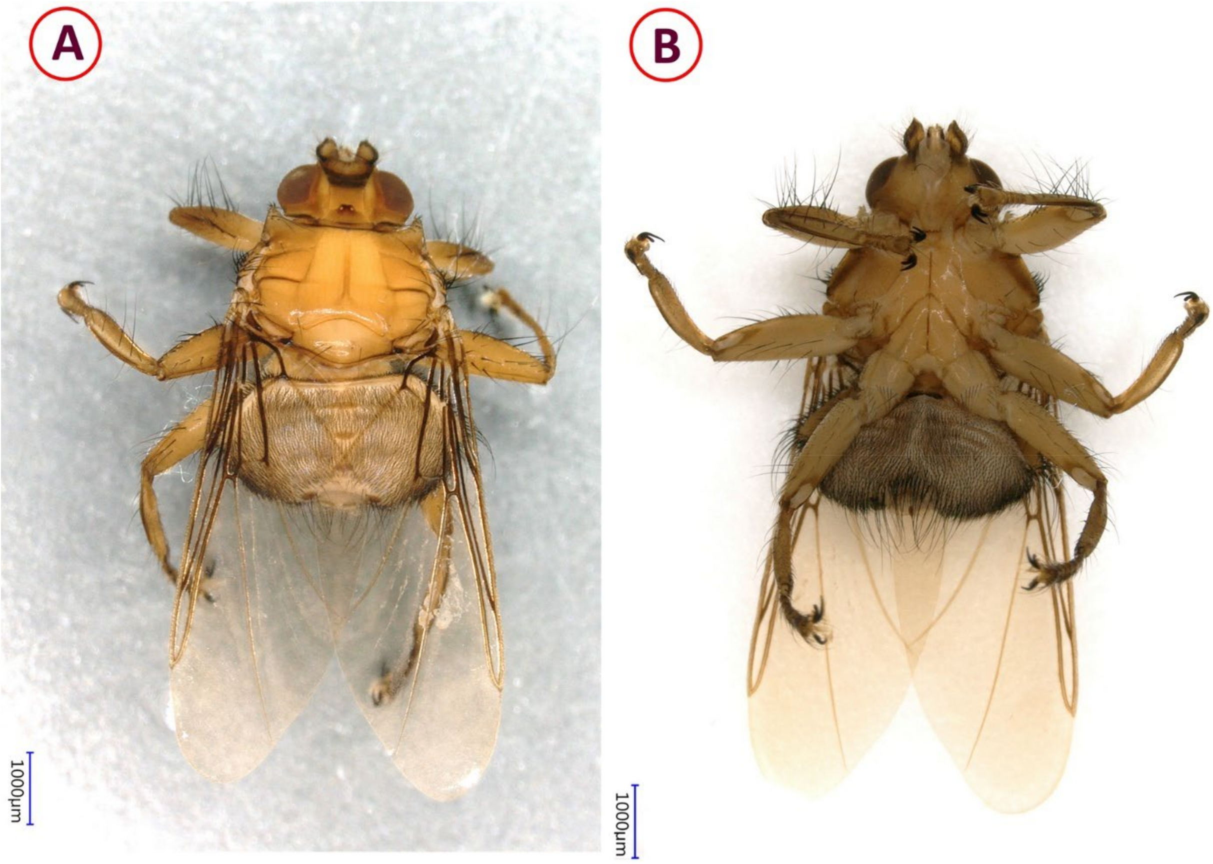
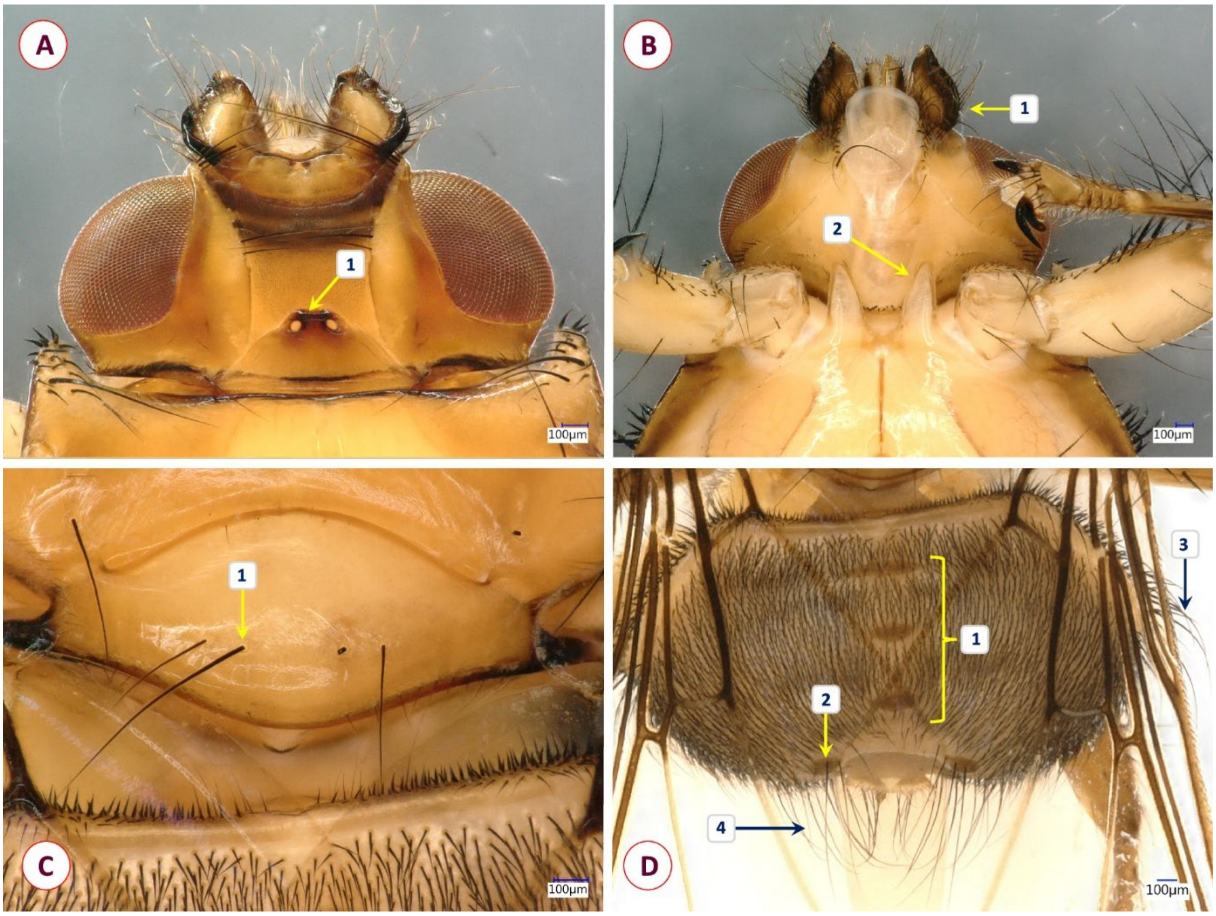


Figure 9. Key morphological characters of the louse fly *Ornithoctona laticornis*. **A** Dorsal view of the head (1 denotes the anterior ocellus situated slightly above the level of posterior eye margins). **B** Ventral view of the head, mesosternal processes (1 denotes the antennae, which were twice as long as broad; 2, the length of the mesosternal process). **C** Scutellum with four prominent hairs (1 denotes the medial hairs, which were twice as long as the lateral ones), **D** Dorsal view of the abdomen (1 denotes three median tergal plates; 2, two log hairs on both plates of tergite six; 3, antero-lateral area of abdomen with long hair; 4, caudal area of abdomen with long hair).



Ornithomya avicularia (n=168) was the most abundant louse fly during the study period, as 71% of the found louse flies belonged to this species. The most common host of this species was Savi's Warbler (*Locustella luscinioides*) (n_{birds}=29, n_{flies}=36) (Table 10). *Ornithomya avicularia* specimens were collected from 26 different bird species of three orders (Passeriformes, Strigiformes, Piciformes) (Figure 10**,** Figure 11).

Figure 10. Taxonomy of the host species of the louse flies Ornithomya avicularia **(A)**, Ornithomya fringillina **(B)** and Ornithoica turdi **(C)** visualized on dendrograms.

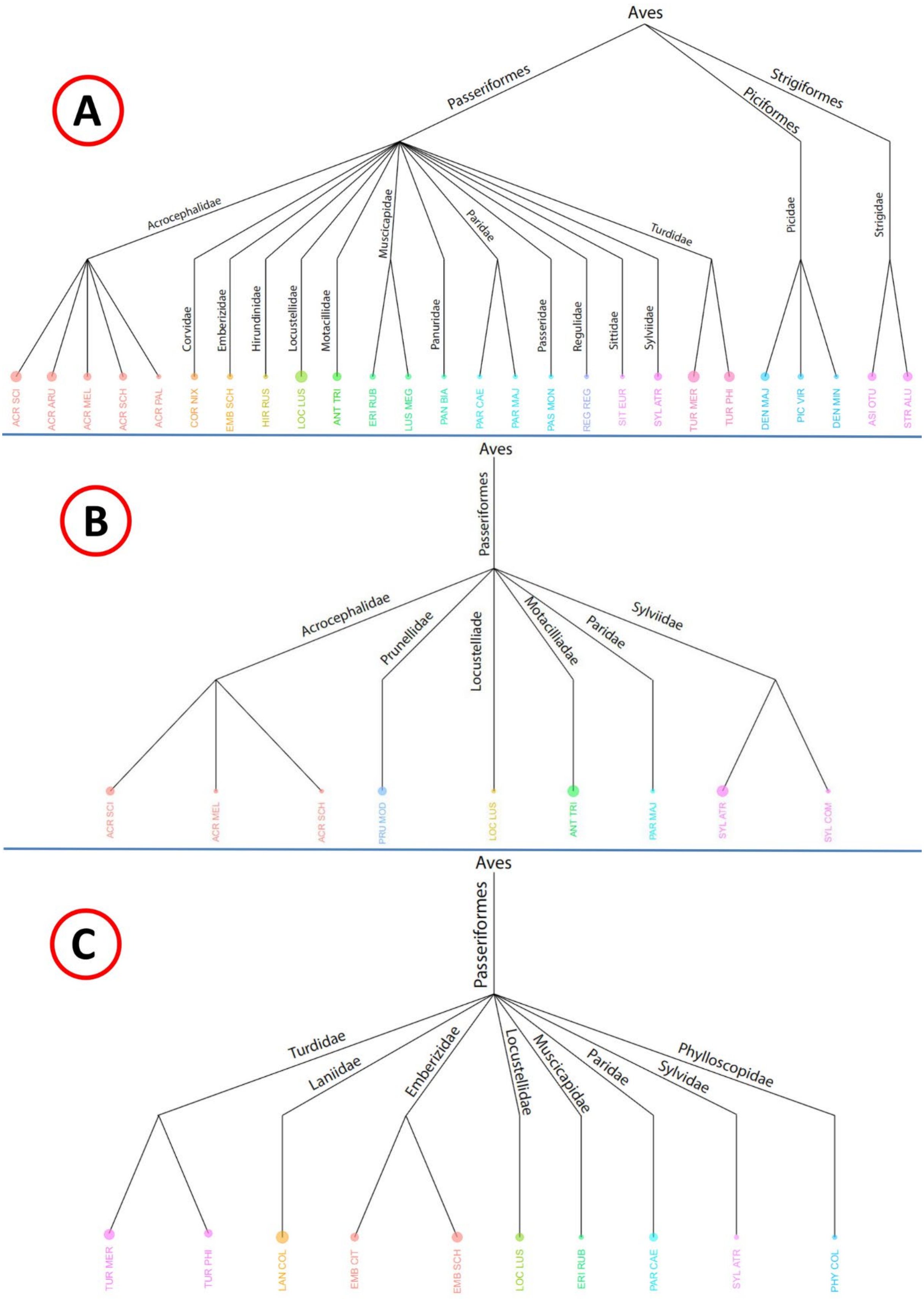
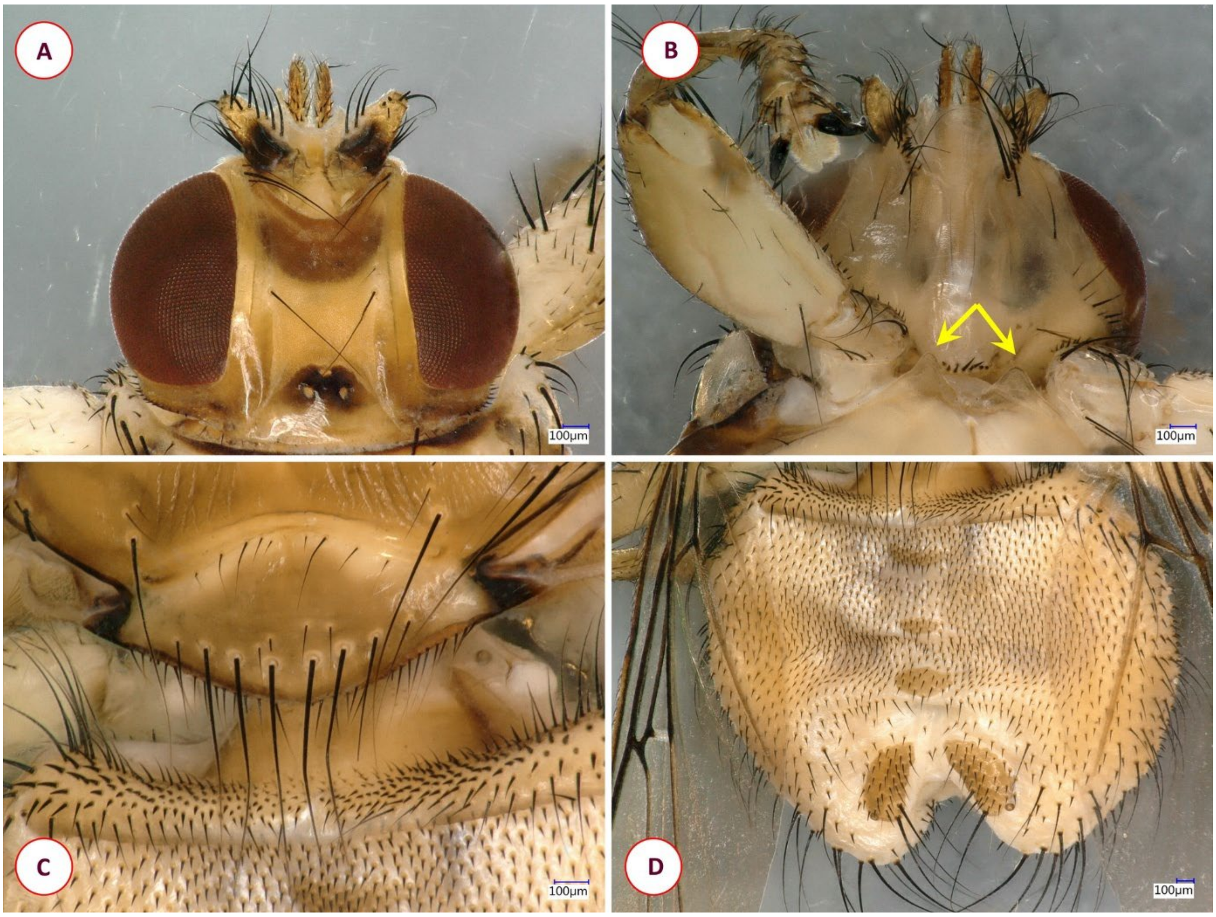
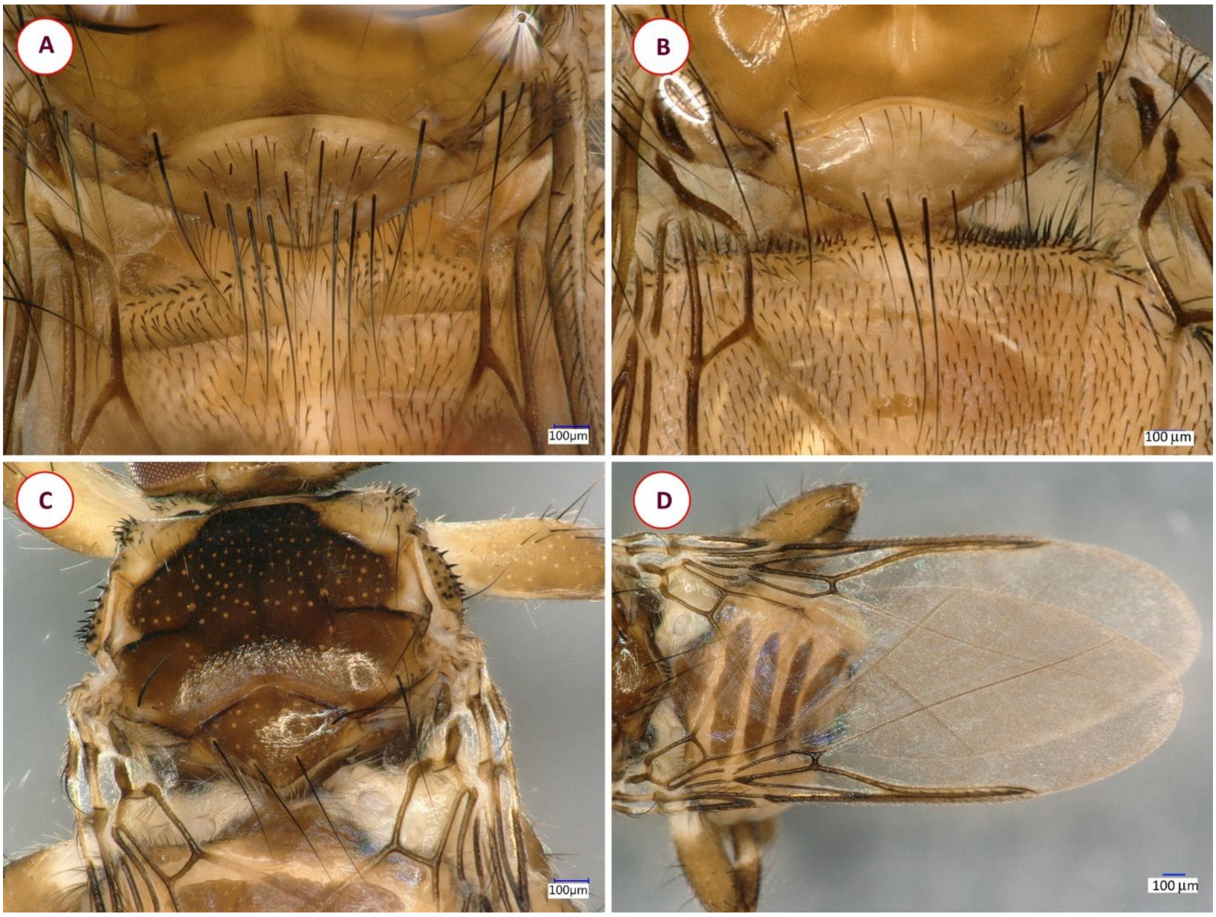


Figure 11. Key morphological characters of the louse fly *Ornithomya avicularia*. **A** Dorsal view of the head. **B** Ventral view of the head, mesosternal processes (arrows). **C** Scutellum. D dorsal view of the abdomen.



Ornithomya biloba (n=23) were collected from Barn Swallow (*Hirundo rustica*) (n_{birds}=20, n_{flies}=21) and from Sand Martin (n_{birds}=1, n_{flies}=1), and one from the environment (Table 10, Figure 12).

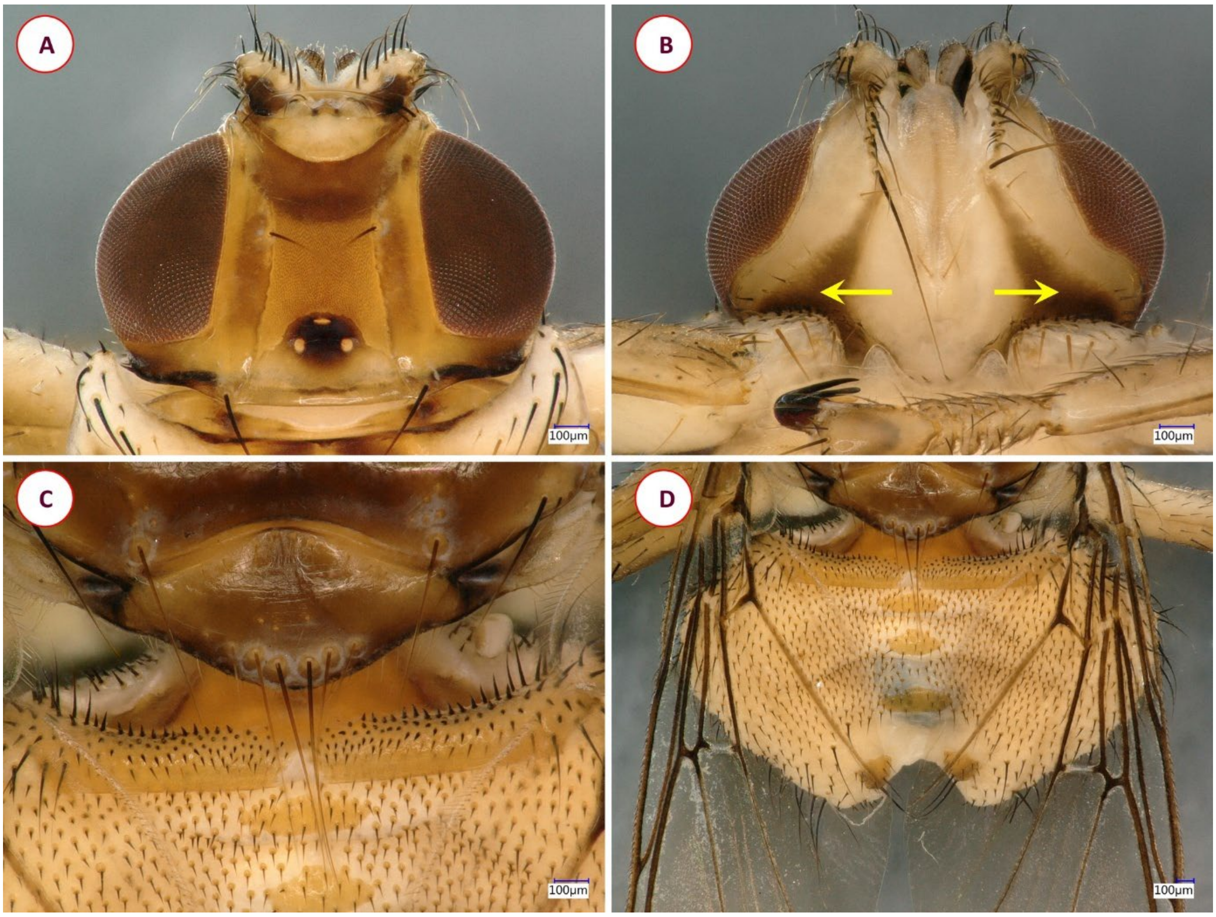
Figure 12. The scutellum of the louse flies **A** *Ornithomya biloba* and **B** *Ornithomya fringillina*. **C, D**: Key morphological characters of Ornithoica turdi: **C** dorsal view of the thorax, scutellum, **D** wings.



Ornithomya fringillina (n=17): Fifteen specimens were removed from nine different passeriform bird species among which the most abundant were the Eurasian Blackcap (*Sylvia atricapilla*) (n_{birds}=3, n_{flies}=3) and the Tree Pipit (*Anthus trivialis*) (n_{birds}=3, n_{flies}=3). Two specimens were collected from the environment (Table 10, Figure 10, Figure 12).

Ornithomya chloropus (n=3). In total, three specimens of this species were collected: from a Dunnock (*Prunella modularis*) (n_{bird}=1, n_{fly}=1), from a Bearded Reedling (*Panurus biarmicus)* (n_{bird}=1, n_{fly}=1) and one from the environment (Table 10, Figure 13).

Figure 13. Key morphological characters of the louse fly *Ornithomya chloropus*. **A** Dorsal view of the head. **B** Ventral view of the head showing sharp, triangular brown spots (arrows). **C** Scutellum. **D** Dorsal view of the abdomen.



Ornithoica turdi (n=25) was the second most abundant species, however, they accounted for only 10.5% of all louse flies. The most common host of this species was the Red-backed Shrike (*Lanius collurio*) (n_{birds}=5, n_{flies}=7). *Ornithoica turdi* have been found feeding on 10 different bird species during the study period (Table 10, Figure 10, Figure 12).

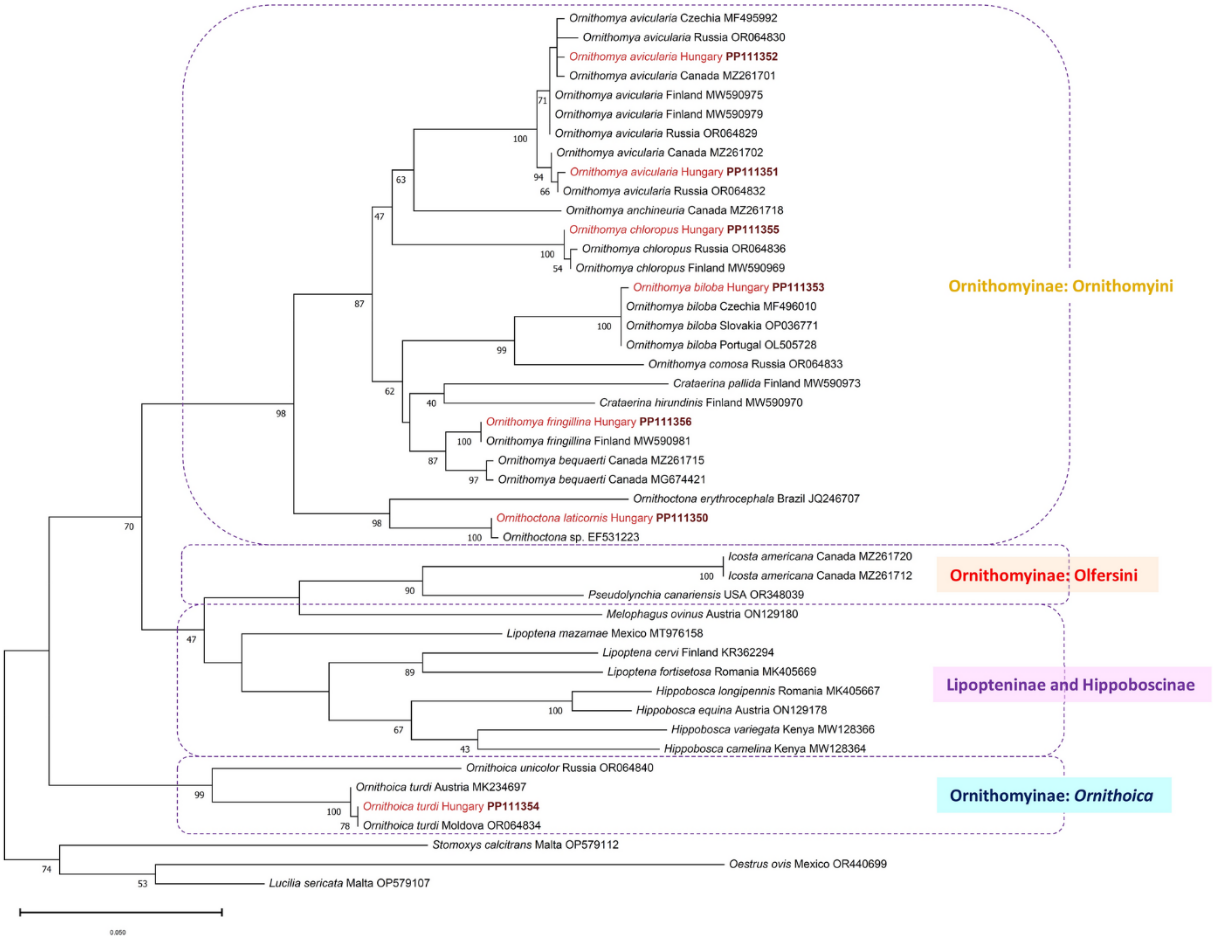
4.5.2 Molecular identification and phylogenetic analyses

In general, based on the cox1 gene of representative specimens, the identity of all six species was confirmed (*O. avicularia*: n=2, *O. biloba*: n=1, *O. fringillina*: n=1, *O. chloropus*: n=1, *O. turdi*: n=1 and *O. laticornis*:n=1).

In particular, *O. laticornis* (PP111350) showed 99.83% identity to an *Ornithoctona* sp. (EF531223) from the collection of the North Carolina State University (host and collection site are unknown).

According to their cox1-sequences, the two *O. avicularia* specimens (PP111351 and PP111352) belonged to different haplotypes, (98.28% identity). PP111351 showed 99.69% identity to *O. avicularia* (OR064832) from Russia and 99.53% to *O. avicularia* (MZ261702) from Canada. PP111352 showed 99.69% identity to *O. avicularia* (OP035933) from Slovakia [37], and the same percent of identity to multiple *O. avicularia* specimens from Canada (MZ261701, MZ261708, MZ261714) (Figure 14).

Figure 14. Phylogenetic tree based on the cytochrome c oxidase subunit I (cox1) gene of hippoboscid flies. The evolutionary history was inferred using the maximum likelihood method and general time reversible (GTR) model.



Ornithomya biloba (PP111353) was 99.84% identical to *O. biloba* specimens from the Czech Republic (MF496010), Slovakia (OP036771) and from Portugal (OL505728) (Figure 14).

Ornithoica turdi (PP111354) showed 100% identity to *O. turdi* (OR064834) from Moldova, and 99.69% to *O. turdi* (MK234697) from Austria (Figure 14).

Ornithomya chloropus (PP111355) showed 99.84% identity to *O. chloropus* specimens from Finland (MW590960, MW590969) and from Russia (OR054225) (Figure 14).

Ornithomya fringillina (PP111356) showed 100% identity to *O. fringillina* specimens from Finland (MW590981, MW590974, MW590963) (Figure 14).

4.5.3 Statistical analyses

Due to the low numbers of *O. chloropus* and *O. laticornis*, no statistical probes were performed involving these species. We have also excluded *O. biloba,* as its host specificity towards the Hirundinidae family would have led to biased (or obvious) results.

According to our analyses, there were significant differences between the host habitats (reed, forest, meadow, forest/meadow) of *O. avicularia* and *O. turdi* (p<0.0001). *Ornithomya avicularia* was the most abundant on reed associated birds, while *O. turdi* was the most commonly found on forest- and meadow-associated hosts. In the case of *O. avicularia* and *O. fringillina*, the result of the same comparison was nonsignificant (p=0.2958). The difference between *O. fringillina* and *O. turdi* was also non-significant (p=0.1985) (Table 11).

Table 11. Number of louse flies according to the habitat of their hosts.

Louse fly species	**Reed-associated birds (R)**	**Meadow-associated birds (M)**	**Forest-associated birds (F)**	**F/M**
Ornithomya avicularia	78	5	35	36
Ornithomya fringillina	5	1	6	3
Ornithoica turdi	5	9	8	3

Comparisons were made, based on the migration habits (resident, resident/short-distance migrants, short-distance migrants and long-distance migrants) of the hosts of *O. avicularia, O. fringillina* and *O. turdi.* The difference between the hosts of *O. avicularia* and *O. fringillina* was significant (p=0.0036) as we found no *O. fringillina* on short-distance migrants. There wass nosignificant difference in the case of the hosts of *O. avicularia* and *O. turdi* (p=0.4033). A significant difference was also visible in the cases of the hosts of *O. fringillina* and *O. turdi,* as the latter was frequently found on short-distance migrants. (p=0.0343) (Table 12).

Table 12. Number of louse flies according to the migration habit of their hosts.

Louse fly species	Resident birds (R)	Short-distance migrant (SDM)	R/SDM	Long-distance migrant
Ornithomya avicularia	10	47	18	79
Ornithomya fringillina	1	0	6	8
Ornithoica turdi	2	9	5	9

The avian hosts were also categorized according to their feeding place (Ground, Above ground, Ground/Above ground). There was a significant difference between the hosts of *O. avicularia* and *O. fringillina* (p=0.0024) as *O. fringillina* have not been found feeding on birds belonging to the ”Ground” category during the study period. On the other hand, 36% of *O. avicularia* parasitized birds belonging to the latter category. The difference was also significant in the case of *O. avicularia* and *O. turdi* hosts (p=0.0068) as 64% of the *O. turdi* specimens were found on birds belonging to the ”Ground” category of feeding. The difference between *O. fringillina* and *O. turdi* was also significant (p<0.0001) (Table 13).

Table 13. Number of louse flies according to the feeding place of their hosts.

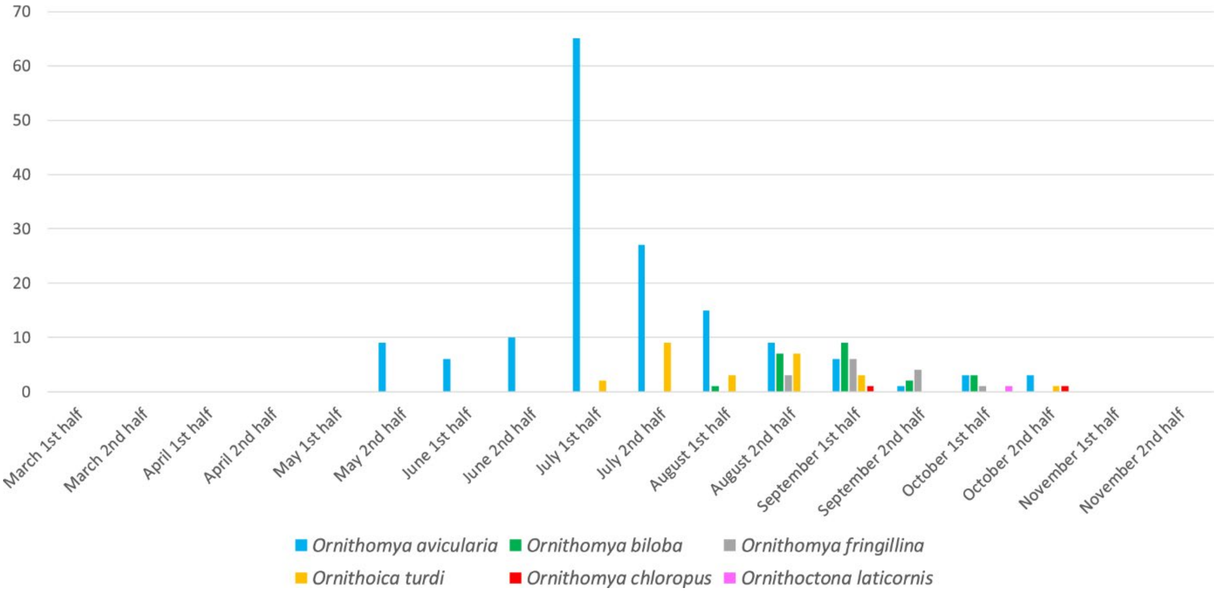
Louse fly species	Ground	Above ground	Ground/Above ground
Ornithomya avicularia	48	93	12
Ornithomya fringillina	0	11	4
Ornithoica turdi	16	9	0

4.5.4 Temporal distribution of louse flies

The temporal distribution of louse fly species found on birds during the eight-year-long study period is visualized in Figure 15. Note, that there was no sample collection in the winter during the presented study. *Ornithomya avicularia* specimens were recovered from the second half of

May, until the end of October, reaching their peak abundance in the first half of July. *Ornithomya biloba* specimens were only collected from the first half of August until the first half of October and were the most common in the first half of September, even though its most common hosts (*Hirundo rustica*) were occasionally caught and checked for the presence of louse flies during springtime. The occurrence of *O. fringillina* was the highest in the first half of September. It was present from the second half of August until the first half of October. *Ornithoica turdi* showed activity from the first half of July until the second half of October, with a peak abundance in the second half of July. Only three specimens of *O. chloropus* were collected - one on 05/09/2022, and one on 31/10/2020. Unfortunately, the precise date of collection was not recorded for the third specimen (but is estimated to be October 2019. *Ornithoctona laticornis* was collected only once, on 09/10/2016.

Figure 15. Temporal distribution of the louse fly species found on birds during the 8-year-long study period.



4.6 Investigation of avian louse flies as potential vectors of protozoan and bacterial pathogens of veterinary importance

Altogether 253 different louse flies were examined during this study. These belonged to nine species. *O. avicularia* (n=138), *O. biloba* (n=29)*, O. fringillina* (n=28), *O. chloropus*, (n=12), *O. turdi* (n=33), *C. hirundinis* (n=1), *C. pallida* (n=8), *Icosta ardeae* (n=3) and *Ornithophila metallica* (n=1).

Coinfections with ticks were observed in the case of 11 flies of the examined, (five *O. avicularia* from four hosts, and six *O. turdi* from six hosts) (Table 14). Coinfection with ticks was significantly more common in the case of *O. turdi* (6 in coinfection/ 27 not in coinfection) than in the case of *O. avicularia* (5/133) (P=0.0076, odds ratio: 0.17). We did not observe tick-coinfection in the cases of the other louse fly species.

Table 14. Birds on which louse fly/tick coinfections were observed.

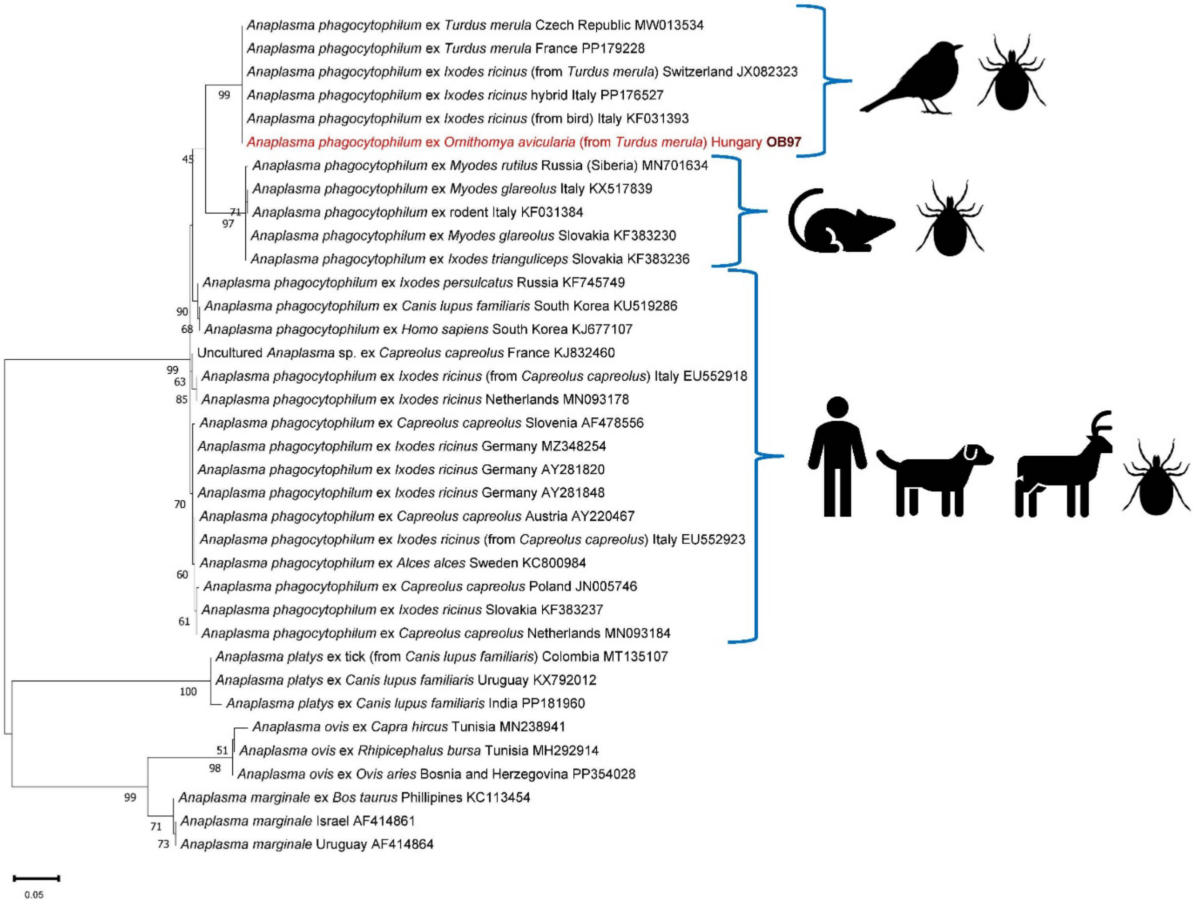
Host bird	Louse fly species(number)	Tick species/stage(number)
TUR PHI	*O. avicularia* (2)	*I. ricinus*/nymph (2) *H. concinna*/nymph (2)
SIT EUR	*O. avicularia* (1)	*I. ricinus*/nymph (1)
LUS MEG	O. avicularia (1)	*I. ricinus*/nymph (1)
LOC LUS	*O. avicularia* (1)	*H. concinna*/larva (2) / nymph (3)
TUR MER	*O. turdi* (1)	*I. ricinus*/nymph (1) *H. concinna*/nymph (2)
TUR PHI	*O. turdi* (1)	*I. ricinus*/larva (1)
LOC LUS	*O. turdi* (1)	*H. concinna*/larva (15) / nymph (1)
LAN COL	*O. turdi* (1)	*I. ricinus*/nymph (1) *H. concinna*/larva (4)
LUS MEG	*O. turdi* (1)	*I. ricinus*/larva (1)
NA	*O. turdi* (1)	*I. ricinus*/larva (1)

According to our analyses, pathogenic *Bartonella, Rickettsia* and *Borrelia* species, as well as piroplasms were completely absent in the examined flies.

Anaplasma sp. was revealed in a single *O. avicularia* specimen, closely resembling *Anaplasma phagocytophilum*, based on a 450 bp long partial sequence of the *groEL* gene. The carrier louse fly was collected from a Blackbird (*Turdus merula*) in Ócsa, on 28.05.2022. This sequence showed 100% identity (450/450 bp) to several *A. phagocytophilum* sequences from Europe (Figure 16). Two of these identical sequences were retrieved from blackbirds: from a skin sample (MW013534) and from a liver sample (PP179228). One sequence was retrieved from an *Ixodes ricinus* larva that was feeding on a blackbird (JX082323). One similar sequence was retrieved from an *Ixodes ricinus* nymph feeding on an unspecified bird in Italy (KF031393).

Finally, a similar sequence was found in a tick, that the author identified as a hybrid of *I. ricinus* and *I. inopinatus* (PP176527). According to our phylogenetic analyses, the latter sequences form a distinct clade separate from those retrieved from mammals.

Figure 16. Phylogenetic tree based on the *GroEl* gene of *Anaplasma* species. The evolutionary history was inferred using the maximum likelihood method and Tamura-Nei model. The pictograms indicate some species the given clade has been described from so far.



Based on the their 16S rRNA genes [264], sequences, resembling *Haematospirillum jordaniae* were retrieved from three *O. fringillina* specimens. All of these flies were collected at Gárdony-Dinnyés. One from a Common Reed Warbler on 22.07.2023, and two from Bearded seedlings (*Panurus biarmicus*) on 09.26.2023. These showed 100% (299/299 bp) identity to MF374623, isolated from Common Reed Warbler (*Acrocephalus scirpaceus*) in Hungary [265], and to several human (*Homo sapiens*) samples, e.g. OM075117 isolated from human blood in Slovenia, OP315756 isolated from human blood in Argentina, or CP014525 isolated in the USA from a human patient.

Based on their *ssu* genes [266], five different genotypes of avian *Trypanosoma* species were revealed (Figure 17). According to our phylogenetic analyses, one of these sequences, that was retrieved from an *O. avicularia* specimen) belongs to the *Trypanosoma bennetti* group (group A) of avian trypanosomes, while the other four genotypes belong to the *Trypanosoma corvi/culicavium* group (group B), specifically to the lineages I, IV, V, and to the recently discovered lineaege B14. The louse flies from which we were able to retrieve *Trypanosoma* sequences, their hosts and collection sites are enlisted in

Table *15*. No sequences belonging to the *Trypanosoma avium*/*thomasbancrofti* group (group C) were detected. A single sequence of *Trypanosoma* sp. was found in an *O. turdi* specimen; however, this sequence was considerably shorter (470 bp) than the rest of our sequences (~820 bp). This showed 100% similarity to several sequences from the *Trypanosoma theileri* group in the GenBank (e.g. OM256597, OM256606, OM256688). This *O. turdi* specimen was collected from an Eurasian Jay (*Garrulus glandarius*) on 17.08.2022 in Csorna, Hungary.

Figure 17. Phylogenetic tree based on the *ssu* gene of Trypanosoma species. The evolutionary history was inferred using the maximum likelihood method and Tamura 3 (T3) model. **(A)** *Trypanosoma bennetti* group; **(B)** *Trypanosoma corvi*/*culicavium* group; **(C)** *Trypanosoma avium*/*thomasbancrofti* group. Numbers indicate lineages, according to the work of Santolíková et al. [304]. The pictograms indicate some important animals the given lieange/group has been described from so far.

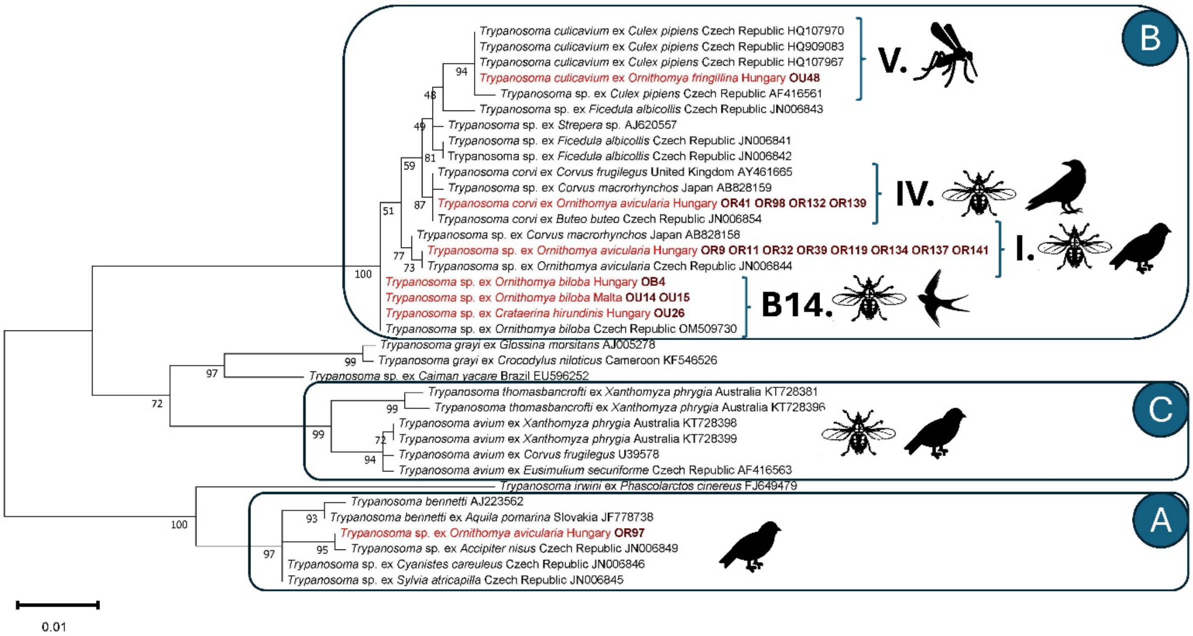


Table 15. Trypanosomes found in louse flies.

***Trypanosoma* species/group/lineage**	**Louse fly species**	**Avian host**	**Collection site**	**Collection date**
Trypanosoma sp., group A	*O. avicularia*	TUR MER	Ócsa, Hungary	28.05.2022
Trypanosoma sp., group B, lineage I.	*O. avicularia*	PIC VIR	Ócsa, Hungary	08.06.2017
Trypanosoma sp., group B, lineage I.	*O. avicularia*	NA	Ócsa, Hungary	04.07.2017
Trypanosoma sp., group B, lineage I.	*O. avicularia*	TUR PHI	Ócsa, Hungary	01.07.2018
Trypanosoma sp., group B, lineage I.	*O. avicularia*	STR ALU	Ócsa, Hungary	01.07.2018
Trypanosoma sp., group B, lineage I.	*O. avicularia*	COR NIX	Barbacs, Hungary	11.07.2022
Trypanosoma sp., group B, lineage I.	*O. avicularia*	PAR MAJ	Veszprém, Hungary	28.06.2022
Trypanosoma sp., group B, lineage I.	*O. avicularia*	ASI OTU	Fehértó, Hungary	25.07.2023
Trypanosoma sp., group B, lineage I.	*O. avicularia*	ACC GEN	Székesfehérvár, Hungary	13.07.2022
Trypanosoma corvi, group B, lineage IV.	*O. avicularia*	TUR PHI	Ócsa, Hungary	06.07.2018
Trypanosoma corvi, group B, lineage IV.	*O. avicularia*	LOC LUS	Ócsa, Hungary	10.07.2022
Trypanosoma corvi, group B, lineage IV.	*O. avicularia*	NA	NA	NA
Trypanosoma corvi, group B, lineage IV.	*O. avicularia*	ACC GEN	Székesfehérvár, Hungary	13.07.2022
Trypanosoma culicavium, group B, lineage V.	*O. fringillina*	ACR SCI	Dinnyés, Hungary	22.07.2023
Trypanosoma sp., group B, lineage B14	*O. biloba*	HIR RUS	Ócsa, Hungary	26.09.2017
Trypanosoma sp., group B, lineage B14	*O. biloba*	HIR RUS	Ghadira, Malta	02.10.2019
Trypanosoma sp., group B, lineage B14	*O. biloba*	HIR RUS	Buskett, Malta	25.09.2020
Trypanosoma sp., group B, lineage B14	*C. hirundinis*	HIR RUS	Dinnyés, Hungary	09.09.2023
Trypanosoma sp. *Trypanosoma theileri* group, lineage ThtII	*O. turdi*	GAR GLA	Csorna, Hungary	17.08.2022

5. Discussion

5.1 Hard ticks (Acari: Ixodidae) associated with birds in Europe: review of literature data

The review data on the ixodid tick infestation of birds were collected from nearly 200 papers published since 1952. In this period, 37 hard tick species (17 from Prostriata and 20 from Metastriata) were reported from 16 orders of avian hosts in Europe. These include endophilic tick species that are ornithophilic (*I. arboricola*, *I. caledonicus*) or of those that prefer mammalian hosts, such as rodents (*I. acuminatus*), carnivores, or insectivores (*I. canisuga*, *I. hexagonus*). Some of the tick species have a clear host preference for sea birds and predominate in Western-Northern Europe (*I. rothschildi*, *I. unicavatus*, *I. uriae*). A significant number of ixodid species are rarely found in association with birds, as exemplified by *D. reticulatus*, *D. marginatus*, *H. erinacei*, *H. parva*, *H. sulcata*, *R. annulatus*, *R. turanicus*, *R. sanguineus*, and *H. aegyptium*. The latter is a tortoise-associated tick species, whereas *R. turanicus* and *R. sanguineus* are mostly reported from birds of prey, most likely transferring from rodent and other prey items to these birds. In addition, exotic (non-indigenous) tick species transported by birds from Africa to Europe include *H. truncatum*, *A. lepidum*, *A. marmoreum*, *A. nuttalli* and *A. variegatum*.

The primary aim of this checklist is to provide a comprehensive reference source (baseline data) for future studies, particularly in the context of discovering new tick-host associations after comparison with already published data. Nevertheless, these data also allow a first-hand analysis of general trends regarding how and which developmental stage of ticks tend to infest avian hosts in general. Therefore, five tick species that were frequently reported from birds and show a broad geographical distribution on this continent were selected for statistical comparison (*I. arboricola*, *I. frontalis*, *I. ricinus*, *H. concinna* and *H. marginatum*) (Supplementary Figure 1, Supplementary Table 1).

Considering developmental stages, larvae and nymphs predominate on birds in the case of *I. ricinus*, *H. concinna,* and *H. marginatum* (n=1667 *vs* 37 adults). This is not the case for ornithophilic tick species (*I. arboricola* and *I. frontalis*) from which adult ticks were collected significantly more frequently (n=301 *vs* 115 adults) ($P < 0.0001$). Interestingly, males of generalist tick species occurred significantly more frequently on birds (n=7 *vs* 30 females) than males of ornithophilic tick species (n=5 *vs* 110 females) ($P = 0.009$).

Based on data that did not specify the tick developmental stage, the tick species *I. arboricola* was significantly ($P<0.0001$) more frequently collected from bird species that typically feed above the ground (n=134) than from those feeding at the ground level (n=60). This was not the case for *I. ricinus* (679 *vs* 1064), *I. frontalis* (121 *vs* 216) and *H. concinna* (36 *vs* 63) (Supplementary Table 1). This general tendency on a continental level is in contrast to what was reported from the southern part of Central Europe where *H. concinna* is mostly associated with bird species typically feeding above the ground level [46,192].The chances for finding *H. marginatum* on bird species characterized by either ground-feeding or arboreal feeding were more equilibrated (82 vs 84). This is in line with its active host seeking (hunting) strategy [7].

In addition, considering data from references that included the number of tick developmental stages collected from various bird species, comparison of tick infestations according to five habitat categories of avian hosts (Supplementary Table 1) did not reveal statistically significant associations (data not shown). However, by assigning bird species into two groups (i.e., typically feeding from the ground *vs* rarely occurring at the soil level: Supplementary Table 1), the following differences were found: Larvae, nymphs and females of *I. arboricola* significantly more frequently occur on bird species feeding above the ground (P<0.0001-0.045), than corresponding stages of *I. frontalis*, *I. ricinus* and *H. concinna*. Females of *I. ricinus* are more likely to infest ground-feeding than arboreal bird species (18 *vs* 4) compared to nymphs of this species (507 *vs* 336) (P=0.046). Interestingly, females of *H. marginatum* significantly more frequently associate with bird species feeding above the ground level than with those collecting food on the soil surface (4 *vs* 1) compared to those of *I. ricinus* (4 *vs* 18) (P=0.017) and *I. frontalis* (27 *vs* 61) (P=0.041).

The ecology of bird-infesting tick species [7] is also illustrated here according to avian orders (Supplementary Figure 1), taking into account the ecology (habitat type) and activity (circadian rhythm and feeding level) of most bird species that belong to a certain order [52] (though this has limitations due to difficulties in assigning general traits at this taxonomic level). In this context, *I. arboricola* was only reported from species of avian orders whose members typically use forested habitats and (with the exception of Columbiformes) typically feed above the ground (Supplementary Figure 1). This tick species was also reported from a high number of nocturnal bird species (Strigiformes), although (as an endophilic tick, with preference for tree holes) it is known to detach from diurnal passerine hosts during the night [116]. Except for two bird species from two orders (Falconiformes, Coraciiformes), *I. frontalis* was always reported from avian orders whose members typically (also) feed from the ground level, in both open and forested habitats (Supplementary Figure 1). This is in line with previous data on *I. frontalis* from Central Europe [111]. By contrast, *I. ricinus* was reported from 13 out of 16 avian orders, including several examples with preference for forest or open habitats, and which typically feed at the ground level or higher (Supplementary Figure 1). Similarly, the majority of avian hosts that were reported to be infested with *H. concinna* represent orders that share both open habitat- and forest-dwelling bird species, as well as ground level and arboreal feeders (Supplementary Figure 1). Last but not least, *H. marginatum* was almost exclusively reported from bird species that belong to orders including a significant number of forest dweller bird species and was also collected from a high number of bird species from orders with nocturnal activity (both Caprimulgiformes and Strigiformes: Supplementary Figure 1). This is in agreement with the reported evening activity and occurrence of this tick species in forested habitats [267].

5.2 Long term evaluation of factors influencing the association of ixodid ticks with birds in Central Europe, Hungary

Although there are many similar previous reports from different countries (e.g.[9,99,115,128,149,268]), this study presents one of the longest continuous bird tick collections in Europe. Over an eight-year-long period, 5833 ticks of 10 species were collected from 2395 birds of 51 species. The dataset itself provides a valuable contribution to the field due to its size.

The two most abundant tick species collected were *I. ricinus* (n_{total}=3971) and *H. concinna* (n_{total}=1706). Only subadult stages were found in case of both species. *Ixodes ricinus* has long been known as the most common tick species that feeds on birds in the Palearctic region[25] and is primarily a forests-dwelling tick species [7]. This fact was confirmed by data presented here, as *I. ricinus* occurred most frequently on birds with forest habitat. Interestingly, this was not true for *H. concinna*. According to the literature data, *H. concinna* can be found in a broad range of different habitats, mainly moist, wooded ecosystems, but in reedbeds as well[7,269,270]. However, according to our data, this species mainly parasitized reed-associated birds (1333 *H. concinna* ticks on birds with reed habitat). The difference between the host habitats of *I. ricinus* and *H. concinna* was strongly significant ($p<0.0001$). Furthermore, 933 *H. concinna* ticks were collected from only one bird species, Savi's Warbler. According to Csörgő et al.[51] number of ringed Savi's Warblers present in Hungary between 1951 and 2006 was 32 083 birds. Interestingly the same numbers of the second and third most common hosts from Ócsa (Eurasian Reed Warbler and Sedge Warbler (*Acrocephalus schoenobaenus*)) were over 220 000 for each species. Savi's Warbler had the highest level of median infestation in the case of nymphs, and the second highest in the case of larvae. In our opinion however, larvae are not the greatest indicators in this regard, as a low presence of larvae can be overlooked easily due to the small size of the parasites.

Regarding the migration habit of the hosts of *H. concinna*, and *I. ricinus*, the results were in line with our previous observation[2] on a strongly significant difference between the hosts of the two tick species: *H. concinna* most commonly occurred on long-distance migrants, whereas *I. ricinus* was most frequently collected from short-distance migrant or resident birds. *Haemaphysalis concinna* is a thermophilic tick species. Its larvae and nymphs have a similar period of peak activity (mainly the summer)[270] and its typical avian hosts are reed-associated long-distance migrants[51].

Among the latter, Savi's Warbler was the most common host in Hungary. According to our hypothesis, the feeding habit of this bird species may explain this phenomenon. Savi's Warbler shares a very similar ecological niche with *H. concinna*, because it mainly feeds on small invertebrates near the water surface in reedbeds. This behavior is consistent during the migration period[51], and lakeshore vegetation was reported to be a preferred habitat type of *H. concinna* in Central Europe[270].

Taken together, *H. concinna* subadults apparently share a much more similar ecological niche with Savi's Warbler, than with other reed-associated songbirds. It is important to mention that this difference is only true among avian hosts and does not extend to mammals and reptiles, which are also favored hosts of *H. concinna* [270], especially roe deer[271].

It was previously reported, that birds with larger body mass carry a higher number of *I. ricinus* nymphs[197]. In this study, the mean intensities of infestations with *I. ricinus* and *H. concinna* stages were categorized according to the average body mass of their avian hosts. In the case of *I. ricinus*, the mean intensity of nymphs showed a trend of increase with the average body mass of the hosts, unlike in the case of *H. concinna* nymphs. However, this could not be supported by the results of statistical analyses, because of the following reasons. First, the majority of *H. concinna* ticks were carried by Savi's Warblers, which is a small size bird species. Second, *I. ricinus* occurred most frequently on ground feeding birds which in general have a larger body mass (e.g., Blackbirds). On the other hand, data on the body mass of bird individuals examined for tick-infestation in the present study were not available, and this parameter is known to change significantly even within the same bird species between different seasons.

The temporal distribution of *I. ricinus* and *H. concinna* developmental stages was also analyzed. *Ixodes ricinus* nymphs always reached their peak infestation on birds during the first half of the annual sampling periods throughout the study, whereas larvae reached their highest abundance from July to October. This is likely a consequence of the prolonged development of *I. ricinus* which takes several years in Central Europe[272] implying that nymphs and larvae collected in the same year belonged to different generations. By contrast, the nymphal and larval peak activities of *H. concinna* were always close to each other, i.e., within 0.5-1.5 month over the summer period. This may reflect that a notable portion of these developmental stages belonged to the same generation, particularly when the larval peak preceded the nymphal peak (e.g., in 2015, 2022). This is in line with observations that under temperate climate this tick species can complete one generation in one year if hosts are available[273] On the other hand, *H. concinna* larvae were also found on birds as early as March and April (e.g., in 2016 and 2017), suggesting overwintering in the larval stage and a generation time longer than one year[270].

During the eight-year-long study period, 102 *I. frontalis* ticks were collected (n_{larvae}=52, n_{nymphs}=38, n_{female}=12). According to the known literature data, *I. frontalis* reaches its peak in March and in November[274,275]. In this study, the vast majority of all developmental stages were collected in the second half of March. The absence of a peak in November is likely because the main sample collection period ended at the end of October/beginning of November each year. From November tick collections, there only a scarce and random amount of data. The fact that this tick is the most abundant at the beginning of spring and the end of autumn explains why *I. frontalis* showed association with resident and/or short-distance migrant birds according to our data (Table 5). *I. frontalis* was almost exclusively found on birds with forest- or mixed meadow/forest habitats (98/102) (Table 4).

Altogether 8 specimens of *I. festai*, six females and two males were also collected during the study period. All hosts were Blackbirds and Dunnocks. The same host species were found to be infested in a previous study from another part of Central Europe, Switzerland [100], but literature data are available from multiple other host species as well [25].

Three *Hyalomma* nymphs were found in total. According to our molecular analyses, two were *H. marginatum* and one was *H. rufipes*. Each of these nymphs had 100% sequence identity with at least one specimen reported from the mid-Mediterranean region (Malta), situated along the Adriatic Flyway crossing Hungary toward the north. Thus, these data are highly relevant to their probable geographical origin. *Hyalomma* species are important vectors of sevedunral different pathogens, including the Chrimean-Congo haemorrhagic fever virus[276]. All *Hyalomma ticks* were collected in April (2015, 2016). Findings of *Hyalomma* subadults during the spring migration period are not uncommon in Central Europe[277] and in Ócsa[29]. It is important to note, however, that the monitoring of *Hyalomma*-carrying birds is of great epidemiological importance.

Thirteen *I. lividus* were identified. This tick is the host-specific parasite of Sand Martin, that feeds extremely rarely on other birds[25,92,276]. It is not surprising that we have found all *I. lividus* ticks on Sand Martins. *Ixodes lividus* have been reported from Hungary long before our study[165].

Twenty-eight *Ha. punctata* larvae were found feeding on a single Common quail. *Haemaphysalis punctata* has been already known in Hungary, as an uncommon parasite on birds [112].

Only one *I. arboricola* nymph was collected during this study. This low number is not surprising, since *I. arboricola* is a nidicolous tick that feeds on nestlings during the summer, and therefore adult birds are mostly infested during winter seasons, when roosting [95]. For this study, sample collection period started in March and ended at the beginning of November each year so did not include the peak season for *I. arboricola*.

Lastly, one *D. reticulatus* female on a Blackbird was found in 2022. This tick was not (yet) feeding, and its occurrence is believed to be accidental, though *D. reticulatus* subadults have been found on Blackbirds (among other birds) before [278].

Based on this eight-year survey, the migration distance, the habitat type, and the feeding habit of birds, as well as the seasonal activity of ticks are all important factors determining the role of birds as tick disseminators. *Haemaphysalis concinna* was the most abundant on long-distance migrant, reed-associated, above-ground feeder birds, in contrast to *I. ricinus*, which predominated on resident or short-distance migrant, ground-feeder birds with forest or meadow habitat. In the study region, Savi’s Wabler (*L. luscinioides*) is by far the most common avian host of *H. concinna* larvae and nymphs.

5.3 Ornithological and molecular evidence of a reproducing *Hyalomma rufipes* population under continental climate in Europe

In Hungary, studies on tick-infestations of birds date back to more than half a century [1], and have been extensively performed on annual or tri-annual bases focusing on the same ringing station in the north-central part of the country (Ócsa: [29,30,46]). Similar reports on ticks from avian hosts are available from numerous European countries, as exemplified by Sweden [279], The Netherlands and Belgium [135], Germany [128], or Italy [280]. Relevant studies have also been reviewed recently [25,281]. However, leaving aside opportunistic and sporadic collections of ticks from birds, the present study is the first "horizontal tick survey" from birds in the Carpathian Basin and probably also in a broader geographical context. This implies that ticks were removed, and their species identified at several ringing stations simultaneously in the course of one year, allowing not only the regional comparison of tick burdens carried by birds, but also assessing the significance and need of similar studies on a larger, continental scale.

In this study, six species of ixodid ticks (three prostriate and three metastriate) were collected from birds. The most significant finding related to tick species diversity was the *H. rufipes*-infestation of three long-distance migrant and a resident bird species. *Hyalomma rufipes* is the vector of Crimean–Congo haemorrhagic fever virus, *Babesia occultans*, *Rickettsia aeshlimannii*, *Ehrlichia* spp., *Coxiella burnetii*, *Rickettsia conorii* and *Anaplasma marginale* [276].

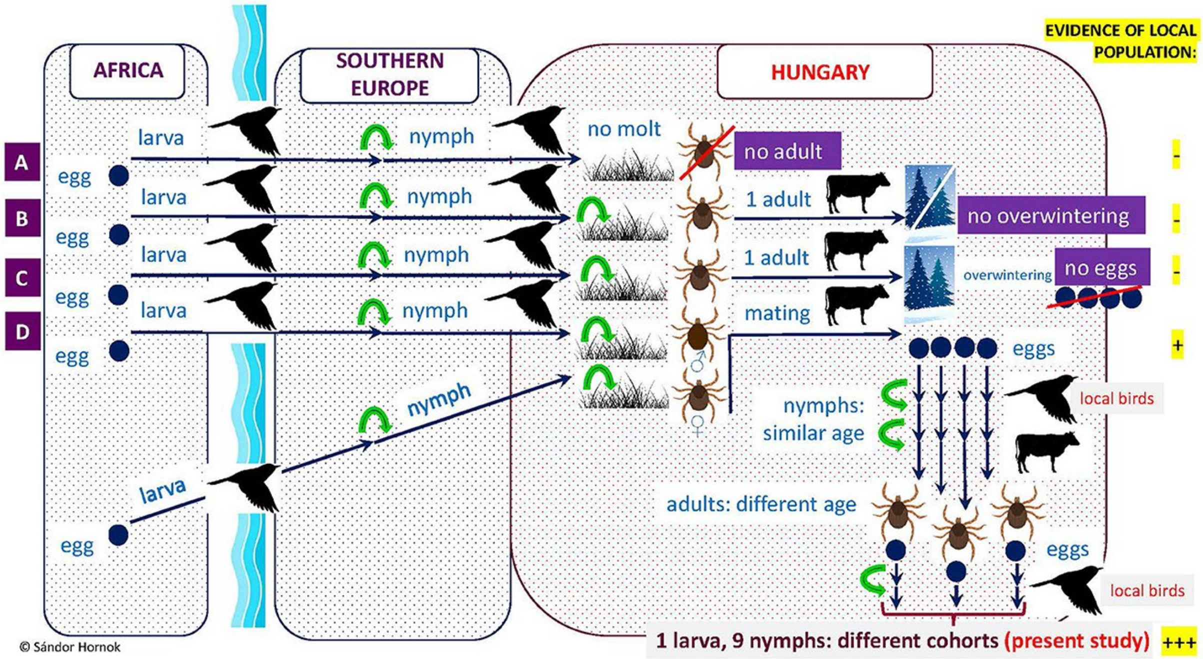
Importantly, *H. rufipes* was collected in south and northwestern Hungary during late spring in 2022, as in a previous study [46]. However, in this study all remaining 10 specimens were removed from birds in the middle of summer (late June) at one ringing station in the southwestern part of the country (Fenékpuszta), i.e., in the same county (Zala) where *Hyalomma*-infestation of a bird was diagnosed for the first time in Hungary in 1955 [1]. In the same region, *Hyalomma* sp. ticks were reported to occur [282] and *H. rufipes* adults were identified on two occasions from cattle [14] (Figure 4.A).

It is utterly unlikely that all five individuals of the two avian host species of these 9 fully engorged nymphs and one unengorged larva of *H. rufipes* (sampled on June 26) carried these ticks into Hungary from abroad. *Hyalomma rufipes* has a two-host life cycle, and engorged nymphs drop off from the host after 21-29 days of infestation [283]. One of the avian hosts shown to harbor nymphs of *H. rufipes* in this study, the Sedge Warbler (*A. schoenobaenus*) typically arrives in Hungary from the wintering grounds in Africa between April and early May [51], and late June (when its *Hyalomma*-infestation was diagnosed) is in the middle of its nesting period, without migration. On the other hand, the other repetitive host of *H. rufipes* in this study, the Bearded Reedling (*P. biarmicus*) is an *a priori* resident bird species, with rarely documented limited movements, but according to ringing data [51] these "vagrancies" never occur in its summer nesting period.

Regarding the results of molecular analyses, it is not surprising that all *H. rufipes* individuals collected in 2022 from birds in Hungary (n=12) had identical 12S rRNA haplotypes, because this genetic marker was shown to be identical in case of a much larger set of *H. rufipes* ticks (n=48) collected from birds with probably different geographical origin [284]. However, in this study the sequenced part of the *cox*1 gene was also identical between all *H. rufipes* (n=11) collected in the Transdanubian part of Hungary, in particular in case of those 10 ticks which were removed from birds at the same ringing station in southwest Hungary (Fenékpuszta). *Hyalomma rufipes* was shown to differ remarkably in its *cox*1 haplotype in case of ticks carried by birds with different geographical origin [284]. Moreover, the ratio and presence or absence of certain *Hyalomma cox*1 haplotypes were demonstrated to be site- and population-specific, usually with multiple haplotypes even within the same population [285]. Therefore, finding of exclusively one *cox*1 haplotype among 10 *H. rufipes* ticks collected in one location (Fenékpuszta) raises the possibility that these ticks represent the same population. Their genetic similarity is probably a consequence of founder effect. Taken together, all three studied mitochondrial, maternally inherited genetic markers were identical only between *H. rufipes* individuals collected in the latter place, also supporting the common maternal aborigine of these ticks.

In addition, the apparently unengorged state of the *H. rufipes* larva on one of these birds also argues against the foreign origin of its tick-infestation. Note that in a previous study only molting (i.e., advanced stage) *H. marginatum* larvae were found on birds in Hungary, and all other stages were nymphs [29,46]. Importantly, hitherto molecularly verified *H. rufipes* larvae were only reported from birds in south European countries (reviewed by Keve et al. [25]), and typically only nymphs of this tick species arrive on birds in countries north of the Mediterranean Basin if these originate from Africa (Figure 18; [25]).

Figure 18. Illustration of the possible consequences of bird-borne transportation of *Hyalomma rufipes* into countries north of the Mediterranean Basin, including Hungary. Green arrows indicate moulting. **(A)** Nymphs transported by birds may die after drop-off, or **(B)** moult to adult which cannot overwinter, or **(C)** if they overwinter as adults, females will not produce eggs in the absence of previous mating, or **(D)** if nymphs carried by birds detach and moult to male and another (carried independently) to female and these meet and mate on cattle, females will be able to lay eggs after drop-off. First generation larvae and nymphs developing from these eggs probably will have a similar state of engorgement but moulting to adults they will find host and will mate at different time. Therefore, existence of a second generation may involve the simultaneous presence of larvae and nymphs of different cohorts on local birds, as shown in this study.



Probably not all ticks carried by migratory birds in the spring were imported by them from southern countries, as they can become infested with ticks of the local fauna, particularly when avian hosts arrive from their wintering grounds during the activity peak of local tick populations. Similarly to previous bird tick studies in the Carpathian Basin [46] and most countries north of the Mediterranean Basin (e.g., [279]), *I. ricinus* was the tick species most commonly collected from birds in 2022 in Hungary. *Haemaphysalis concinna* was the second most abundant tick species on birds, which, however, seems to be unique to the Carpathian Basin and its region [25]. Both of these tick species (*I. ricinus*, *H. concinna*) indigenous to Hungary tend to infest birds which arrive in their main activity periods [286], therefore *I. ricinus* (peak activity: April) is mainly found on residents and short-distance migrants (typically arriving early spring), whereas *H. concinna* (peak activity: May) on long-distance migrants (usually arriving late spring) [51].

New tick-host associations revealed in this study include the presence of *H. rufipes* on the Bearded Reedling (*P. biarmicus*), and infestation of Moustached Warbler (*Acrocephalus melanopogon*) with *H. concinna*. Although *D. reticulatus* seldom occurs on birds [25], its immature developmental stages were reported from avian hosts (including the Common Blackbird, *T. merula*) [278]. The collection of its adult on a Blackbird during this study is probably an accidental finding.

Considering the regional occurrence of tick species on birds in the Carpathian Basin, *H. concinna* is a thermophilic tick species [287], and this is in accordance with its predominance on birds in central-south Hungary during the spring, and central-southeastern Hungary in the autumn (i.e., the warmest regions of the country: Supplementary Figure 3). On the other hand, the reason for the absence of *I. frontalis* from birds in the southern part of Hungary maybe twofold. First, the relevant sampling locations are near water surfaces where the predominant bird species (e.g., Savi's Warbler, *L. luscinioides*) are not known to be hosts or (e.g., the Sedge Warbler, *A. schoenobaenus*) are exceptional hosts of this tick species [25]. Second, in these places bird mist-netting (i.e., tick collection) was terminated sooner than the late autumn peak activity of *I. frontalis* in the relevant region [274].

In this study, *H. rufipes* was only found in the Transdanubian region and once along the southern Danube, in line with the reported 130-year-long endemicity of *Hyalomma* species in the country [4,20,21]. While *Hyalomma*-infestation was previously reported on non-water-associated bird species (*E. rubecula*, *C. communis*) in the springtime in north-central Hungary (Ócsa) [29,46], this is the first occasion when ticks of this genus were observed on reed-dwelling birds in another region of Hungary, in a different season (during summer). This also raises the question on what the differences between the relevant two habitats in terms of landscape, vegetation and avian hosts are.

Fenékpuszta Bird Ringing Station is situated next to Lake Balaton. Here, the reedbed habitat in the riparian zone narrows to about 150 meters at the site of the mist-nets, where 12 pieces of these stretch across the reedbed completely. Due to uninterrupted reeds, this is an important stopover site for migrating passerines, particularly *Acrocephalus*-species. Based on ringing data, mostly long-distance migrant Sedge Warblers (*A. schoenobaenus*) and Eurasian Reed Warblers (*A. scirpaceus*) stop in this area, but Great Reed Warblers (*A. arundinaceus*) and Savi's Warblers (*L. luscinioides*) are also significant in numbers.

Conversely, in Ócsa Bird Ringing Station the heterogeneous reedbed habitats of the capture locations are interspersed with fast growing shrubs as elderberry (*Sambucus nigra*) and blackberry (*Rubus fruticosus*), with softwood stands (*Salix* spp. and *Populus* spp.) forming most of the vegetation. Thus, the Eurasian Blackcap (*Sylvia atricapilla*) and the European

Robin (*Erithacus rubecula*) are two most common short-to-mid-distance migratory species here [31]. Regarding the capture rates of the species groups of migrating passerines, there is a significant difference between the homogeneous reedbed and other habitats (where the reedbed is patchy and alternates with deciduous forests, berry bushes). While *Acrocephalus* spp. account for the largest proportion of birds caught in Fenékpuszta, bush-dwelling warblers present a higher portion in Ócsa.

Based on the above, the existence of at least one indigenous population of *H. rufipes* is evidenced in the western part of Transdanubia, near Lake Balaton, because of the following reasons: (1) most importantly, the recognized avian hosts of *H. rufipes* were extremely unlikely to arrive from abroad shortly prior to their examination, especially not all five of them; (2) one larva was not yet engorged; (3) the larva and the nymphs (in a similar state of engorgement) were offspring of two females and must have belonged to different local generations (Figure 18); and (4) all *H. rufipes* found in the relevant location were identical in their haplotypes based on three maternally inherited mitochondrial markers, probably reflecting founder effect.

In addition, adults of *H. rufipes* are known to occur in the western part of the Carpathian Basin for 130 years, and in the same county (Zala) with its present collections adults of this tick species were found to infest cattle repeatedly [14]. Small local populations of *H. rufipes* were proposed to explain the occasional presence of *H. rufipes* in Russia [288,289] and its populations in scattered areas are also known in north Africa [289,290]. However, to our knowledge, this is the first report of a similar phenomenon and its evidence from Europe. One of the most important limiting factor for the survival of this xerophilic tick species under any climate is thought to be the maximum level of precipitation (annual rainfall) which is around 650 mm in southwestern Hungary (Supplementary Figure 3), i.e., similar to what is well-tolerated by *H. rufipes* in its range within Africa [291,292]. Populations of these ticks probably can survive winter conditions as adults in southwestern Hungary where winter temperatures are among the mildest in the country (Supplementary Figure 3). Nevertheless, *H. rufipes* is known to have populations in regions with up to 120 days of frost [289]. It is also noteworthy here that the likely overwintering of *H. rufipes* was reported in the Czech Republic [15], north of Hungary. Importantly, the discovered *H. rufipes* population might act as a "stepping-stone" for this tick species during its northward transportation by birds which use the relevant habitat near Lake Balaton in southwestern Hungary as a stopover site (see above).

On the other hand, no evidence was gained for any further *Hyalomma* populations indigenous in other regions of Hungary, as also indicated by the overall absence of *Hyalomma* ticks from birds in the autumn migration period. Thus, also taking into account the over-century-long presence of adult *Hyalomma* ticks, up to now there was no evidence for their emergence in the Carpathian Basin, but here evidence is reported for the emergence of a local population for the first time.

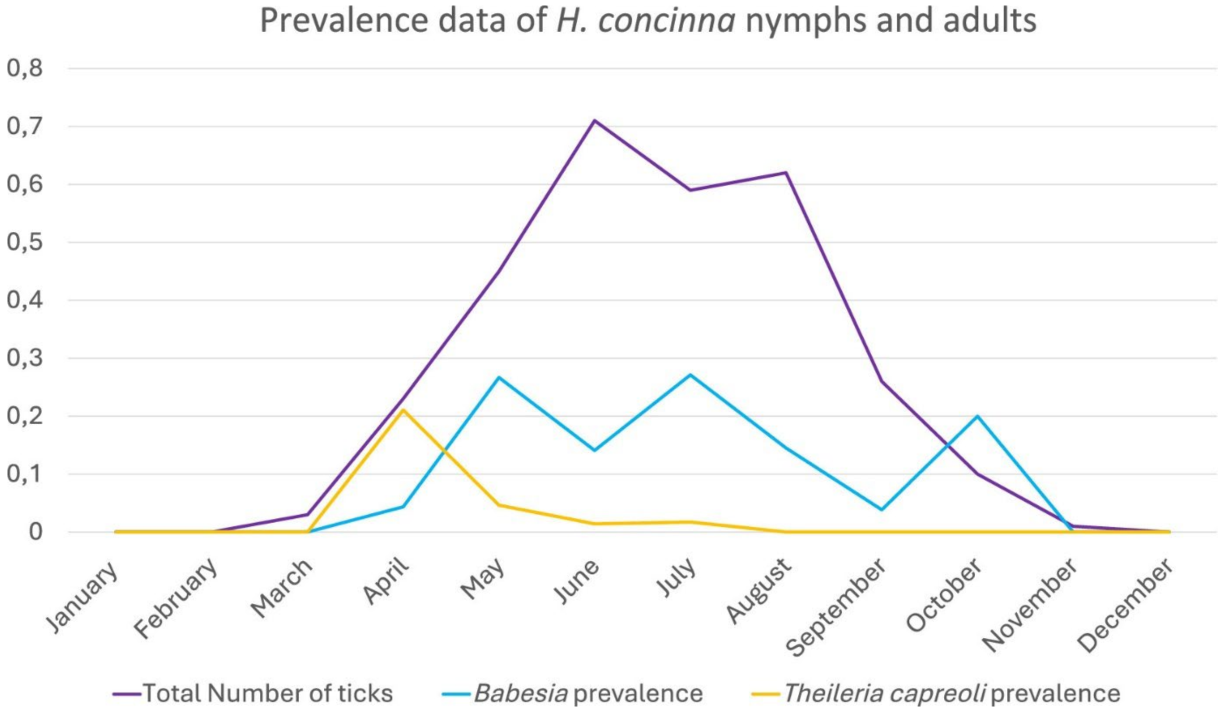
Similarly relevant to a broader, international context, the most important aim of the present study was also fulfilled, i.e., it was successful to demonstrate discrepancies between sampling sites, indicating that in the above context single-site surveys may be biased (not informative) on the actual risk posed by birds in transporting ticks in a geographical region or country. Therefore, to assess the emergence or increasing presence of a *Hyalomma* species, ticks should be collected (larvae and nymphs from birds, and/or adults from reproductive hosts) extensively and annually in different regions of suspected endemic areas, preferentially by unbiased professionals who should stick to a standard methodology (sampling protocol).

5.4 Uneven temporal distribution of Far-Eastern piroplasms (Piroplasmida: Babesiidae, Theileriidae) in *Haemaphysalis concinna* in an urban biotope of the Western Palearctic focus region of this tick species

This study aimed to evaluate the seasonal prevalence of *H. concinna*-associated piroplasms in an urban habitat situated in a hotspot of the Palearctic range of this tick species (Rubel et al., 2018). In total, one *Theileria* species, and eleven *Babesia* genotypes were detected, the latter likely representing at least four different species based on their phylogenetic clustering (Figure 6).

During this study, *T. capreoli* was not detected in questing (pre-feeding) *H. concinna* larvae, but only in nymphs and adult ticks, probably in accordance with its transstadial maintenance. The latter implies that in the absence of transovarial transmission the first opportunity for a tick to obtain theileriae is from the host, during feeding as larvae, ensuring the transstadial survival of these piroplasms when tick larvae molt to the nymph stage [293]. *Theileria capreoli*-infected *H. concinna* nymphs and adults predominated in April and May (Figure 19), meaning a significant association with the springtime. Interestingly, the peak of horizontal movements of roe deer, the most important mammalian hosts of *H. concinna* (Hornok et al., 2012) also tends to be in May owing to territorial fights (Markolt et al., 2012), thus coinciding with this seasonality. This phenomenon, the seasonally biased occurrence of a tick-borne piroplasm is very similar to what was observed in another urban biotope of the same city, where the presence of *B. canis* in its vector, *D. reticulatus* was almost exclusively noted in the late winter-early spring period [294].

Figure 19. The Babesia prevalence and the *Theileria capreoli* prevalence in *H. concinna* nymphs and adults, and the total numbers of H. concinna nymphs and adults. The total numbers of ticks were divided by 100 to adjust them to the graph.



Within the family Babesiidae, all *Babesia* genotypes identified in this study belong to the phylogenetic group associated with ruminant hosts (Figure 6). These genotypes are commonly referred to as "Far Eastern Babesia genotypes" due to their initial discovery and reporting in the Far East regions of Irkutsk (Siberia) and the Khabarovsk region of Russia [295]. The majority of these genotypes identified in *H. concinna* were previously reported from this tick species in the Far East (denoted as “Hc” in Figure 6), with the exception of one genotype from *Ixodes persulcatus* (“Ip” in Figure 6).

In this study, *Babesia* sp. Bp-Hc2 and *Babesia* sp. Bp-Hc8 were detected in nymphs and adults of *H. concinna*. This, together with the absence of these babesiae from larvae likely indicates that these piroplasms arrived in *H. concinna* larvae which fed on migratory birds and are not endemic in the examined urban biotope. This is confirmed by data attesting to the association of ticks harboring these two piroplasms with birds that have historical (evolutionary-phylogenetic) or actual (migratory) connection with the Far East, as exemplified by *Emberiza citrinella* and *Luscinia* spp. [26,296]. Sequence analysis of their 18S rRNA gene segments (PQ040347 and PQ040353) revealed that these sequences are identical to those previously reported from the Far East. [295].

On the other hand, *Babesia* sp. Bp-Hc5 and *Babesia* sp. Bp-Hc7 were only found here in questing *H. concinna* larvae, indicating transovarial transmission and the likely indigenous status of these piroplasms. This is corroborated by the presence of these species in roe deer (*C. capreolus*) sampled in Italy [297], and in *H. concinna* collected from local wild boars (*Sus scrofa*) in Hungary [298]. This finding is especially significant considering the zoonotic nature of the latter *Babesia* genotype [299]. The *Babesia* genotypes, of which only larvae or larvae and nymphs of *H. concinna* were found to be PCR-positive (*Babesia* sp. Bp-Hc3), most likely represent well-established, indigenous species, as is also reflected by the different genetic variants with single nucleotid polymorphism (Figure 5), likely resulting from mutations during reproduction.

Babesia infection in *H. concinna* nymphs and adults was significantly more common in May and in July compared to the other months of the year. This early predominance of infected ticks and consequent decline of their ratio towards the end of tick season was already reported in the case of other tick-borne pathogens, as exemplified by *Anaplasma phagocytophilum*, *Borrelia burgdorferi* sensu lato, *Rickettsia helvetica* and even *B. canis* (Kantsø et al., 2010; Mysterud et al., 2013; Hornok et al., 2016). Considering potential mechanisms underlying these observations, it was reported that (1) *B. burgdorferi* can prolong the survival of infected *Ixodes ricinus* [300]; (2) *Babesia bovis* increases the activity, thus host finding of *Rhipicephalus microplus* by interfering with tick metabolism [301]; and (3) *Babesia microti* may promote its tick-borne transmission by enhancing the feeding success of *Ixodes trianguliceps* (Randolph, 1991). Further studies will be necessary to clarify this in the case of babesiae carried by *H. concinna*.

In conclusion, results of this study show for the first time that in a questing population of *H. concinna* the highest monthly prevalence of *Babesia* and *Theileria* spp. may be different from each other and from the peak abundance of carrier ticks, and ticks harboring pathogens predominate early in the annual tick activity period. Based on previous reports on the effect of tick-borne pathogens on other tick species, the factors that may influence this phenomenon in *H. concinna* may include changes in the metabolism, behavior (host finding and feeding success), as well as survival rate of infected ticks.

5.5 Contributions to our knowledge on avian louse flies (Hippoboscidae: Ornithomyinae) with the first European record of the African species *Ornithoctona laticornis*

Six bird-associated louse fly species were identified and analyzed. For several species no molecular or host-related data have been available or evaluated from most Central European or European countries. Therefore, our results compensate for hitherto missing information on the ecology and phenology of relevant louse fly species in this geographical region. In addition, host-related factors of louse-fly infestation, as well as the taxonomic uniformity of this group were also addressed here.

According to our best knowledge, this is the first time, that *O. laticornis* has been found in Europe. It was suggested by Hutson in 1984 [44] that the European appearance of this louse fly species could be expected, since it had been found on multiple Palearctic migrants in Africa. However, it was only reported from Central and South Africa [302] and from Madagascar [56] so far. Interestingly enough, our specimen was found feeding on a Blue Tit on 09/10/2016, which is long after the spring migration period. Not much is known about the life cycle of *O. laticornis*, but other hippoboscid adults can survive for around 4 months, and the duration of the pupal stage varies from 19 to 23 days in the summer and 20-36 days in the winter [303], also, bird specific louse flies tend to overwinter in pupal form in Europe, which may indicate even longer pupal stages [48]. The pupae of hippoboscids (in general) usually can be found in bird nests, on the hair of mammalian hosts, or on the ground [32]. According to this information, we hypothesize that a bird carried an imago from Africa during the spring migration, and the adult fly survived until October in Hungary. However, due to the relatively large temporal distance (~5-7 months) between the spring migration of birds (March-May) and the finding of the *O. laticornis* specimen , it is also conceivable, that an already fertilized female *O. laticornis* had arrived on a migrating bird in the spring and had been able to lay a larva ready to pupate that later hatched in Hungary. In the latter case, probably a second-generation imago was found. The other hypothesis is suggested by Hutson in his work from 1984 [44]: *Ornithoctona laticornis* can occasionally be found in Europe, but due to its close morphological resemblance to *O. avicularia* (Figure 9, Figure 11) some specimens were misidentified before. According to European keys, the morphological similarity with *Ornithomya rupes* maybe even more deceiving [32]. Therefore, already existing population(s) of *O. laticornis* might be present in Europe. Regrettably, we do not have enough information to draw accurate conclusions, however, regardless of how this specimen came to Hungary, the fact that it was found on a resident bird is proof that *O. laticornis* can survive Central European conditions, not just in the Summer, but in the Autumn as well. This finding highlights the importance of comprehensive research on wild bird parasites, as due to the migratory nature of their hosts, these animals can be indicators of the direct effects of climate change.

Other species, identified as (*O. avicularia O. fringillina, O. biloba, O. chloropus and O. turdi*) have all been reported in Hungary before [49]. The euryxenous natures of *O. avicularia*, *O. turdi* and *O. fringillina* have long been known, as has the host specificity of *O. biloba* towards the Hirundinidae family (especially the Barn Swallow) [39,45,49,304–306].

Ornithomya avicularia was the most abundant louse fly in the presented study, the second most abundant was *O. turdi*, followed by *O. biloba*, *O. fringillina*, and *O. chloropus*. Another, similar and recent study from another Central European country, the Czech Republic, had different relative abundancies [304], for instance, *O. biloba* and other stenoxenous species were represented in much larger numbers. The main reason for this difference is, that in the mentioned study, nestlings of Barn Swallows and Swifts (*Apus apus*) were also checked for potential louse flies. Therefore, not only have they collected an enormous amount of *O. biloba* specimens but have also found other stenoxenous louse flies in the nests of the latter birds, namely *Crataerina hirundinis* and *Crataerina pallida*. In our study, no bird nests were examined and Barn Swallows were only occasionally caught, which explains the relatively low number of *O. biloba,* as due to the random nature of the sample collection, the relative presence of *O. biloba* (and other hosts-specific species) is also highly affected by the relative number of swallows among the examined hosts.

This study reports the first nucleotide sequence of *O. laticornis* (PP111350). Although our sequence showed 99.83% identity to an *Ornithoctona* sp. (EF531223), its host and site of origin are unknown (from the collection of the North Carolina State University). The closest relatives (that is available in the GenBank database) of our *O. laticornis* (PP111350) specimen are the previously mentioned *Ornithoctona* sp. (EF531223) [307] and *Ornithoctona erythrocephala* from Brazil (JQ246707) [308], based on their cox1 genes (Figure 14).

The genus *Ornithoica* seems to show a more distant genetic relationship to genera belonging to the subfamily Ornithomyinae (*Ornithomya*, *Ornithoctona*, *Icosta*, *Pseudolynchia*, *Crataerina*) than certain representatives of the subfamilies Hippoboscinae (*Hippobosca equina*, *Hippobosca longipennis, Hippobosca variegata*) and Lipopteninae (*Lipoptena mazamae*, *Lipoptena cervi*, *Lipoptena fortisetosa* and *Melophagus ovinus*) according to their cox1 genes (Figure 14). This is in line with a recent report from Russia [309]. As shown in a previous study: [308] this statement is also true when the phylogenetic analysis is based on the 18S ribosomal rDNAs as well. These results suggest, that the genus *Ornithoica* might belong to a different subfamily, and the taxonomy of Ornithomyinae should be revised.

According to our statistical analyses, the migration habit, the habitat type and the feeding habit of birds affect their potential role as louse fly hosts in Hungary. Three euryxenous louse fly species were examined in these regards. Significant differences were found between the migration habits of the hosts of *O. avicularia* and *O. fringillina.* In a previous study from the Czech Republic, significant difference was found between the migration habit of the two species' hosts as well, however in the cited study *O. avicularia* was far less common on long-distance migrant birds than on short-distance migrants [304]. In a study from Finland, no significant difference was found in this regard [43]. This might suggest, that host preference patterns may differ under different climates, or the migratory habit alone cannot explain host specificity patterns, but other factors (e.g. ornithological and geographic) may influence the results as well. Nevertheless,both species were the most common on long-distance migrants, and only differed by their ratios. The difference between the hosts of *O. avicularia* and *O. turdi* in the same context was not significant, however, the difference between the hosts *O. turdi* and *O. fringillina* was again significant. The latter significance may strengthen the results of the previous two tests.

The habitat-association of hosts also seemed to be different in the case of *O. avicularia* and *O. turdi* ($p<0.0001$), as *O. avicularia* was the most common on reed associated birds, and *O. turdi* was the most abundant on forest- and meadow-associated birds. The difference was less pronounced and non-significant between *O. avicularia* and *O. fringillina*, and between *O. fringillina* and *O. turdi* as well. In contrast with this, both *O. avicularia* and *O. fringillina* preferred birds with forest habitat, but were uncommon on birds from ”wetlands” in Finland [43].

Birds were categorized according to their feeding place as well. Interestingly, each comparison demonstrated significant differences (*O. turdi vs O. avicularia*, *O avicularia vs O. fringillina* and *O. fringillina vs O. turdi*). These results show, that despite the fact that all of the three statistically examined hippoboscid species have developed wings and are able to fly [44,309], their host selection is influenced by the hosts feeding height. Specifically, *O. turdi* predominated on birds feeding at ground level, whereas *O. fringillina* was absent on birds exclusively feeding at ground level. *Ornithomya avicularia* was approximately twice as abundant on birds feeding above ground compared to those feeding on the ground. (Table 13)

Most of the louse fly species (*O. turdi, O. fringillina, O. chloropus)* are the most active at the end of the summer and in the autumn. *Ornithomya biloba* flies have been only collected during the autumn migration of its hosts (Barn Swallow, and other species of Hirundinidae). During the spring migration and the roosting season, none of the previously mentioned louse fly species were found, despite the fact that in other countries *O. biloba* had been found on early swallows [310]. The appearance of *O. avicularia* preceded all other louse flies, as this species was active from the second half of May, and remained active during the sample collection period. This means that this species was the only one that was found to be active on foraging birds during the main nesting season (Figure 15). It is important to note, that our sample collection started in March and ended in November each year. Although this interval includes the spring (March-May) and autumn migration (September-November) periods [311], only randomly caught birds were examined for the presence of louse flies, and no bird nests were checked during the study. Therefore, these results are only relevant to the activity of flies on flying and/or foraging birds, except the wintering period.

This is the first report of *O. laticornis* in Europe, as well as the first molecular-phylogenetic analysis of this species. In accordance with previous studies, the migration habit, the habitat type and the feeding habits of birds affect their potential role as the hosts of *O. avicularia*, *O. fringillina*, and *O. turdi,* but these patterns may differ in different geographical regions. According to our analyses and the available literature data, members of the genus *Ornithoica* show distant phylogenetic clustering to genera belonging to the subfamily Ornithomyinae (where it was hitherto assigned), necessitating taxonomic revision of this group in the near future.

5.6 Investigation of avian louse flies as potential vectors of protozoan and bacterial pathogens of veterinary importance

In this study, 253 specimens of 9 different louse fly species were analysed. Most of these flies were originated from several areas across Hungary. Six *O. biloba and a single O. metallica* were collected in Malta during a previous research [284], while three *O. avicularia* specimens were originated from Norway. Some flies that were analysed in a different context in a previous study were also used here [312].

While pathogen transmission during co-feeding is a known phenomenon in the case of ticks [313], it is not known whether ticks can infect louse flies via the same route. Based on our results however, tick and louse fly co-infection is relatively rare, we only observed it in the case of two species, *O. avicularia* and *O. turdi* (Table 14), with the latter coinfecting birds with ticks more commonly. Different species of louse flies feeding on the same bird is also uncommon in Central Europe, where co-feeding of louse flies of different species (only *O. avicularia* and *O. turdi*) was observed only on two out of 175 infested birds [312].

Based on our results we suspect that the role of avian louse flies in the transmission of pathogenic *Bartonella, Rickettsia, Anaplasma*, *Borrelia* specie*s,* as well as piroplasms is either non-existent or minimal in the evaluated region. This is partially in contrast to previous results [314] where the authors examined eight *O. biloba* and 12 *O. avicularia* specimens, and found three different *Babesia* species in the latter. Based on the fact, that this study was performed in a neighbouring country of Hungary (Slovakia), and the fact that we were unable to find any piroplasms despite analysing eleven times more *O. avicularia*, and the fact that the latter species seldom feeds on mammalian host [315] suggest that these previous findings are either results of contamination or an accidental consumption of infected bloodmeal. We find it unlikely, that members of the subfamily *Ornithomyinae* would play a role in the transmission of piroplasms.

We were able to retrieve a sequence closely resembling *A. phagocytophilum* from an *O. avicularia* specimen collected from a Blackbird. Interestingly, this sequence formed a distinct clade in the *A. phagocytophilum* group, with low support, confirming the results of Baráková et al. (2014), Lesiczka et al. (2021) and Rouxel et al. (2024). The sequences belonging to this clade, are related to Blackbirds (liver and skin samples: PP179228 and MW013534) [317,318], or ticks feeding on blackbirds (JX082323) and on a non-defined avian host (KF031393) [316]. A single sequence was retrieved from a tick collected from the environment. Since we found this sequence in only a single *O. avicularia,* it cannot be proven that louse flies serve as biological vectors of this pathogen, but it is now heavily suspected that a clade of *A.*

phagocytophilum exists that is related to blackbirds (and potentially other birds as well). A recent study shed light upon the fact that Blackbirds yielded the highest number of *A. phagocytophilum* infested ticks in the examined population in Sweden [319]. However, in the same study, only 0.9% of the ticks collected from migratory birds were infected. In a study conducted in France, 680 birds of 11 eleven species were analysed for the presence of *A. phagocytophilum*, and only Blackbirds were found to be infested (three out of 91 birds) [318]. This sequence is identical to the *A. phagocytophilum* sequence of this study. In South-Korea 7/40 (17.5%) birds belonging to the Turdidae family were found to be infested with *A. phagocytophilum* [320]. It has to be stated however, that in Europe, Blackbirds are very frequent hosts of *Ixodes ricinus*, the main vectors of *A. phagocytophilum* in Europe [25,321]. In fact, in Hungary, Blackbirds are the most common hosts of *I. ricinus* [322]

Trypanosoma species on the other hand were common in our sample population, similarly to as reported by Santolíková et al., 2022. We were able to detect six different genotypes based on the *SSU* gene (

Table *15*). Five of these belonged to the avian Trypanosomes, namely to the *Trypanosoma bennetti* group, and to the *Trypanosoma corvi*/*culicavium* group. No sequences from the *Trypanosoma avium*/*thomasbankrofti* group were revealed. (Figure Y) A single, sequence was found in an *Ornithoica turdi* specimen, which showed the highest similarity (100%) to several members of the *Trypanosoma theileri* group (ThII). Members of this lineage are reported to infect bovines and deers, while the vectors can be several Dipteran species, likely mosquitoes [323]. Since this sequence was considerably shorter than the rest of our *Trypanosoma* sequences (470 vs 820 bp) we did not included it in our phylogenetic analysis. The recently discovered *Trypanosoma* lineage B14 [42] was revealed from several *O. biloba* specimens from Hungary and Malta, revealing a broad geographical distribution in Europe (

Table *15*). This result further strengthens the theory that this lineage of the genus *Trypanosoma* may affect mainly the Barn swallow (*H. rustica*) in Europe, as we detected this protozoon from another stenoxenous parasite of the latter bird species for the first time, namely *C. hirundinis*. It must be mentioned that this lineage has been found in several predator birds in Thailand prior to our study [42]. Similarly to Santolíková et al., [42], the most common *Trypanosoma* genotypes isolated from avian louse flies belonged to the *Trypanosoma corvi*/*culicavium* group, lineages I. and IV. In contrast to the latter study however, no sequences from the recently discovered B13 lineage were found among our samples. On the other hand, a single sequence of *Trypanosoma culicavium* (lineage V) was found in an *O. fringillina* specimen for the first time. The role of avian louse flies in the transmission of several *Trypanosoma* species is heavily suspected. In the superfamily Hippoboscoidea ("Pupipara"), this would be not unprecedented, as tsetse flies (Glossinidae) are biological vectors of *Trypanosoma* species [324].

Haematospirillum jordaniae was detected in three *Ornithomya fringillina* specimens. All these flies were collected at the same sample collection site, at Gárdony-Dinnyés in 2023. Two flies were feeding on Bearded reedlings, and one on a Common Reed Warbler. Interestingly, Hornok et al. found this bacteria in the blood of the latter bird species in Central Hungary, in 2017 [325]. A short sequence that showed close resemblance to *H. jordaniae* was also retrieved from an *O. chloropus* specimen that was collected from a Dunlin in Fertőújlak, Hungary. While *H. jordaniae* was discovered in 2016 [326], it is now considered an emerging pathogen of medical importance [327]. While not much is known about this bacterium, it seems to affect mainly middle aged or senior men, and is related to fresh water [327,328]. For example, in a recent case report, a Slovenian man was supposedly infected in Hungary, while he had cut himself with a reed during fishing activity at a lake [328]. Therefore, it is not surprising that all *H. jordaniae* sequences were detected in louse flies that were feeding on reed-associated birds. Little is known about the pathogenic effect of this bacterium on birds, and further studies are needed to assess the reservoir (or potentially vector) role of *O. fringillina* (and potentially *O. chloropus*) in relation to this bacterium.

In conclusion, this study presents one of the most extensive pathogen-focused investigations on avian louse flies conducted in Europe to date. A total of 253 individual flies representing nine species were examined for the presence of *Bartonella*, *Borrelia burgdorferi* sensu lato, members of the families Rickettsiaceae and Anaplasmataceae, as well as Piroplasmida and *Trypanosoma* species. Based on our results, we suggest that avian louse flies (Hippoboscidae: Ornithomyinae) play a limited role in the transmission of the examined bacterial pathogens and piroplasms. However, the findings of this study further emphasize the potential role of avian louse flies in the transmission of *Trypanosoma* species. To the best of our knowledge, this is the first report of the blackbird-associated *A. phagocytophilum* strain in an avian louse fly, specifically in *O. avicularia*. In addition, this study reports, for the first time, the presence of the newly described *Trypanosoma* lineage B14 in both Hungary and Malta, as well as in the louse fly *C. hirundinis*. Furthermore, we document for the first time the presence of *T. culicavium* (in *O. fringillina)*, a *Trypanosoma* species from the "bennetti group" (in *O. avicularia)*, and *H. jordaniae* (in three specimens of *O. fringillina)* in hippoboscid flies. A *Trypanosoma* species from the "theileri group" was also identified for the first time in an avian louse fly, *O. turdi*. These findings contribute important new data to our understanding of the pathogen-host associations and vector potential of avian louse flies.

6. New scientific findings

1. The role of Savi's warbler as the most prominent avian host of *Haemaphysalis concinna* in Hungary was revealed for the first time.

2. First detection of a reproducing *Hyalomma rufipes* population in Europe.

3. First revelation of the uneven temporal distribution of piroplasms in an urban *Haemaphysalis concinna* population.

4. First detection of the African louse fly *Ornithoctona laticornis* in Europe.

5. First time detection of *Anaplasma phagocytophilum* in a member of *Ornithomyinae* subfamily (*Ornithomya avicularia*)

6. First time detection of *Trypanosoma* sp., lineage B14 in Hungary and Malta, as well as in *Crataerina hirundinis*.

7. First time detection of *Trypanosoma culicavium*, *Trypanosoma* sp. (from the “theileri” group), and *Trypanosoma* sp. (from the “bennetti” group) from members of the Ornithomyinae subfamily.

8. First time detection of *Haematospirillum jordaniae* in hippoboscid flies.

7. References

[1] Janisch M. Kullancsgazda madarak különféle betegségek közvetítői [Tick carrier birds spreading disease agents]. Aquila 1960;67–68:191–4.

[2] Keve G, Csörgő T, Benke A, Huber A, Mórocz A, Németh Á, et al. Ornithological and molecular evidence of a reproducing *Hyalomma rufipes* population under continental climate in Europe. Frontiers in Veterinary Science 2023;10:272.

[3] Sonenshine DE. The Biology of Tick Vectors of Human Disease. Tick-Borne Diseases of Humans, John Wiley & Sons, Ltd; 2005, p. 12–36.

[4] Karpelles L. Adalékok Magyarország atka-faunájához faunájához [Contributions to the mite-fauna of Hungary]. Mathematikai és Természettudományi Közlemények 1893;25:439–41.

[5] Grimm NB, Staudinger MD, Staudt A, Carter SL, Chapin III FS, Kareiva P, et al. Climate-change impacts on ecological systems: introduction to a US assessment. Frontiers in Ecology and the Environment 2013;11:456–64. https://doi.org/10.1890/120310.

[6] Rochlin I, Toledo A. Emerging tick-borne pathogens of public health importance: a mini-review. J Med Microbiol 2020;69:781–91. https://doi.org/10.1099/jmm.0.001206.

[7] Estrada-Peña A, Mihalca AD, Petney TN. Ticks of Europe and North Africa: A Guide to Species Identification. Springer; 2018.

[8] Hoogstraal H, Kaiser MN, Traylor MA, Gaber S, Guindy E. Ticks (Ixodoidea) on birds migrating from Africa to Europe and Asia. Bulletin of the World Health Organization 1961;24:197.

[9] Brinck P, Svedmyr A, von Zeipel G. Migrating birds at Ottenby Sweden as carriers of ticks and possible transmitters of tick-borne encephalitis virus. Oikos 1965:88–99.

[10] Capek M, Literak I, Kocianova E, Sychra O, Najer T, Trnka A, et al. Ticks of the *Hyalomma* marginatum complex transported by migratory birds into Central Europe. Ticks Tick Borne Dis 2014;5:489–93. https://doi.org/10.1016/j.ttbdis.2014.03.002.

[11] Hansford KM, Carter D, Gillingham EL, Hernandez-Triana LM, Chamberlain J, Cull B, et al. Hyalomma rufipes on an untraveled horse: Is this the first evidence of *Hyalomma* nymphs successfully moulting in the United Kingdom? Ticks and Tick-Borne Diseases 2019;10:704–8.

[12] Uiterwijk M, Ibanez-Justicia A, van de Vossenberg B, Jacobs F, Overgaauw P, Nijsse R, et al. Imported Hyalomma ticks in the Netherlands 2018-2020. Parasites Vectors 2021;14:244. https://doi.org/10.1186/s13071-021-04738-x.

[13] Grandi G, Chitimia-Dobler L, Choklikitumnuey P, Strube C, Springer A, Albihn A, et al. First records of adult *Hyalomma marginatum* and *H. rufipes* ticks (Acari: Ixodidae) in Sweden. Ticks Tick Borne Dis 2020;11:101403. https://doi.org/10.1016/j.ttbdis.2020.101403.

[14] Hornok S, Horváth G. First report of adult *Hyalomma marginatum rufipes* (vector of Crimean-Congo haemorrhagic fever virus) on cattle under a continental climate in Hungary. Parasit Vectors 2012;5:170. https://doi.org/10.1186/1756-3305-5-170.

[15] Rudolf I, Kejikova R, Vojtisek J, Mendel J, Penazziova K, Hubalek Z, et al. Probable overwintering of adult *Hyalomma rufipes* in Central Europe. Ticks Tick-Borne Dis 2021;12:101718. https://doi.org/10.1016/j.ttbdis.2021.101718.

[16] Wallménius K, Barboutis C, Fransson T, Jaenson TG, Lindgren P-E, Nyström F, et al. Spotted fever Rickettsia species in *Hyalomma* and *Ixodes* ticks infesting migratory birds in the European Mediterranean area. Parasites & Vectors 2014;7:1–20.

[17] Földvári G, Szabó É, Tóth GE, Lanszki Z, Zana B, Varga Z, et al. Emergence of Hyalomma marginatum and *Hyalomma rufipes* adults revealed by citizen science tick monitoring in Hungary. Transboundary and Emerging Diseases 2022.

[18] Bah MT, Grosbois V, Stachurski F, Muñoz F, Duhayon M, Rakotoarivony I, et al. The Crimean-Congo haemorrhagic fever tick vector *Hyalomma marginatum* in the south of France: Modelling its distribution and determination of factors influencing its establishment in a newly invaded area. Transboundary and Emerging Diseases 2022;69:e2351–65.

[19] Krézsek C, Bally AW. The Transylvanian Basin (Romania) and its relation to the Carpathian fold and thrust belt: Insights in gravitational salt tectonics. Marine and Petroleum Geology 2006;23:405–42.

[20] Kotlán S. Adatok a hazai kullancs-fauna ismeretéhez [Data on the Hungarian tick fauna]. Állattani Közl 1919;18:33–6.

[21] Kotlán S. A hazai kullancsok rendszere [The Classification of the Ticks of Hungary]. Állattani Közlöny 1921;20:43–50.

[22] Gryczyńska A. Urban and Forest-Living Blackbirds Turdus merula as Hosts of Borreliella spp. Infected Ticks. Pjoe 2018;66:309–14. https://doi.org/10.3161/15052249PJE2018.66.3.010.

[23] Kaiser MN, Hoogstraal H, Watson GE. Ticks (Ixodoidea) on migrating birds in Cyprus, fall 1967 and spring 1968, and epidemiological considerations. Bulletin of Entomological Research 1974;64:97–110.

[24] Hasle G. Transport of ixodid ticks and tick-borne pathogens by migratory birds. Frontiers in Cellular and Infection Microbiology 2013;3.

[25] Keve G, Sandor AD, Hornok S. Hard ticks (Acari: Ixodidae) associated with birds in Europe: Review of literature data. Front Vet Sci 2022;9:928756. https://doi.org/10.3389/fvets.2022.928756.

[26] Flaisz B, Sulyok KM, Kováts D, Kontschán J, Csörgő T, Csipak Á, et al. Babesia genotypes in *Haemaphysalis concinna* collected from birds in Hungary reflect phylogeographic connections with Siberia and the Far East. Ticks Tick Borne Dis 2017;8:666–70. https://doi.org/10.1016/j.ttbdis.2017.04.013.

[27] Hornok S, Flaisz B, Takács N, Kontschán J, Csörg\Ho T, Csipak Á, et al. Bird ticks in Hungary reflect western, southern, eastern flyway connections and two genetic lineages of Ixodes frontalis and *Haemaphysalis concinna*. Parasites & Vectors 2016;9:1–9.

[28] Hornok S, Kováts D, Csörgő T, Meli ML, Gönczi E, Hadnagy Z, et al. Birds as potential reservoirs of tick-borne pathogens: first evidence of bacteraemia with Rickettsia helvetica. Parasit Vectors 2014;7:128. https://doi.org/10.1186/1756-3305-7-128.

[29] Hornok S, Csörgő T, de la Fuente J, Gyuranecz M, Privigyei C, Meli ML, et al. Synanthropic birds associated with high prevalence of tick-borne rickettsiae and with the first detection of *Rickettsia aeschlimannii* in Hungary. Vector Borne Zoonotic Dis 2013;13:77–83. https://doi.org/10.1089/vbz.2012.1032.

[30] Hornok S, Karcza Z, Csörgő T. Birds as disseminators of ixodid ticks and tick-borne pathogens: note on the relevance to migratory routes. Ornis Hungarica 2012;20:86–9. https://doi.org/10.2478/orhu-2013-0010.

[31] Csörgő T, Harnos A, Rózsa L, Karcza Z, Fehérvári P. Detailed description of the Ócsa Bird Ringing Station, Hungary. Ornis Hungarica 2016;24:91–108.

[32] Oboňa J, Sychra O, Greš S, Heřman P, Manko P, Roháček J, et al. A revised annotated checklist of louse flies (Diptera, Hippoboscidae) from Slovakia. Zookeys 2019;862:129–52. https://doi.org/10.3897/zookeys.862.25992.

[33] Nartshuk EP, Matyukhin AV, Shokhrin VP, Markovets MY. New records of ornithophilous louse-flies (Diptera: Hippoboscidae: Ornithomyinae) from the Russian Far East. Far Eastern Entomologist 2019;384:15–20.

[34] Maa TC. A revised checklist and concise host index of Hippoboscidae (Diptera). Pacific Insects Monograph 1969;20:261–99.

[35] Lee L, Tan DJX, Oboňa J, Gustafsson DR, Ang Y, Meier R. Hitchhiking into the future on a fly: Toward a better understanding of phoresy and avian louse evolution (Phthiraptera) by

screening bird carcasses for phoretic lice on hippoboscid flies (Diptera). Systematic Entomology 2022;47:420–9. https://doi.org/10.1111/syen.12539.

[36] Farajollahi A, Crans WJ, Nickerson D, Bryant P, Wolf B, Glaser A, et al. Detection of West Nile virus RNA from the louse fly *Icosta americana* (Diptera: Hippoboscidae). Journal of the American Mosquito Control Association 2005;21:474–6.

[37] Čisovská Bazsalovicsová E, Víchová B, Oboňa J, Radačovská A, Blažeková V, Králová-Hromadová I. Bird Louse Flies *Ornithomya* spp. (Diptera: Hippoboscidae) as Potential Vectors of Mammalian *Babesia* and Other Pathogens. Vector-Borne and Zoonotic Diseases 2023;23:275–83. https://doi.org/10.1089/vbz.2022.0088.

[38] Peña-Espinoza M, Em D, Shahi-Barogh B, Berer D, Duscher GG, Van Der Vloedt L, et al. Molecular pathogen screening of louse flies (Diptera: Hippoboscidae) from domestic and wild ruminants in Austria. Parasites Vectors 2023;16:179. https://doi.org/10.1186/s13071-023-05810-4.

[39] Rekecki T, Rajkovic D. Diversity and prevalence of ornithophilic louse flies (Diptera: Hippoboscidae: Ornithomyinae) in Serbia. Turkish Journal of Zoology 2023;47:261–7. https://doi.org/10.55730/1300-0179.3138.

[40] Andreani A, Belcari A, Sacchetti P, Romani R. Antennal morphology and fine structure of flagellar sensilla in Hippoboscid Flies with special reference to *Lipoptena fortisetosa* (Diptera: Hippoboscidae). Insects 2022;13:236.

[41] Svobodová M, Volf P, Votýpka J. Trypanosomatids in ornithophilic bloodsucking Diptera. Med Vet Entomol 2015;29:444–7. https://doi.org/10.1111/mve.12130.

[42] Santolíková A, Brzoňová J, Čepička I, Svobodová M. Avian Louse Flies and Their Trypanosomes: New Vectors, New Lineages and Host–Parasite Associations. Microorganisms 2022;10:584. https://doi.org/10.3390/microorganisms10030584.

[43] Lehikoinen A, Pohjola P, Valkama J, Mutanen M, Pohjoismäki JLO. Promiscuous specialists: Host specificity patterns among generalist louse flies. PLoS One 2021;16:e0247698. https://doi.org/10.1371/journal.pone.0247698.

[44] Hutson AM. Handbooks for the Identification of British Insects: Keds, Flat-flies and Bat-flies...(hippoboscidae and Nycteribiidae). Royal Entomological Socie; 1984.

[45] Oboňa J, Bazsalovicsová EČ, Pintilioaie A-M, Dumitru V, Gavril OCV, Topală L-E, et al. Checklist of Hippoboscidae (Diptera) from Romania. Historia Naturalis Bulgarica 2023;45:229–38.

[46] Hornok S, Flaisz B, Takács N, Kontschán J, Csörgő T, Csipak Á, et al. Bird ticks in Hungary reflect western, southern, eastern flyway connections and two genetic lineages of Ixodes frontalis and *Haemaphysalis concinna*. Parasit Vectors 2016;9:101. https://doi.org/10.1186/s13071-016-1365-0.

[47] Kemenesi G, Dallos B, Oldal M, Kutas A, Földes F, Németh V, et al. Putative novel lineage of West Nile virus in Uranotaenia unguiculata mosquito, Hungary. VirusDis 2014;25:500–3. https://doi.org/10.1007/s13337-014-0234-8.

[48] Kaufman G. Magyarország kullancslégy fajai és a fecske-kullancslégy biológiája [The louse fly species of Hungary, and the biology of the swallow-louse fly]. Állatorvostudományi Egyetem, 1988.

[49] Papp L. Checklist of the Diptera of Hungary. vol. 1. Hungarian Natural History Museum; 2001.

[50] Hornok S, Flaisz B, Takács N, Kontschán J, Csörgő T, Csipak Á, et al. Bird ticks in Hungary reflect western, southern, eastern flyway connections and two genetic lineages of Ixodes frontalis and *Haemaphysalis concinna*. Parasites & Vectors 2016;9:101. https://doi.org/10.1186/s13071-016-1365-0.

[51] Csörgő T, Karcza Z, Halmos G, Magyar G, Gyurácz J, Szép T, et al. Magyar madárvonulási atlasz [Atlas of bird migration in Hungary]. Budapest: Kossuth kiadó; 2009.

[52] Snow DW, Perrins CM. The Birds of the Western Palearctic. Concise Edition. Oxford Univ. Press 1998.

[53] Hornok S, Meli ML, Gönczi E, Halász E, Takács N, Farkas R, et al. Occurrence of ticks and prevalence of Anaplasma phagocytophilum and Borrelia burgdorferi sl in three types of urban biotopes: forests, parks and cemeteries. Ticks and Tick-Borne Diseases 2014;5:785–9.

[54] Filippova NA. Fauna of Russia and neighbouring countries. Ixodid ticks of subfamily Amblyomminae. vol. 4. St Petersburg, Russia: Nauka Publishing House; 1997.

[55] Contini C, Palmas C, Seu V, Stancampiano L, Usai F. Redescription of the male of Ixodes festai Rondelli, 1926 (Ixodida: Ixodidae) on specimens from Sardinia (Italy). Parasite 2011;18:235–40. https://doi.org/10.1051/parasite/2011183235.

[56] Rahola N, Goodman SM, Robert V. The Hippoboscidae (Insecta: Diptera) from Madagascar, with new records from the "Parc National de Midongy Befotaka." Parasite: Journal de La Société Française de Parasitologie 2011;18:127.

[57] Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Mol Mar Biol Biotechnol 1994;3:294–9.

[58] Black 4th WC, Piesman J. Phylogeny of hard-and soft-tick taxa (Acari: Ixodida) based on mitochondrial 16S rDNA sequences. Proceedings of the National Academy of Sciences 1994;91:10034–8.

[59] Beati L, Keirans JE. Analysis of the systematic relationships among ticks of the genera Rhipicephalus and Boophilus (Acari: Ixodidae) based on mitochondrial 12S ribosomal DNA gene sequences and morphological characters. J Parasitol 2001;87:32–48. https://doi.org/10.1645/0022-3395(2001)087[0032:AOTSRA]2.0.CO;2.

[60] Burkman EJ. Genetic structure of *Amblyomma cajennense* (Acari: Ixodidae) populations based on mitochondrial gene sequences 2009.

[61] Bitencourth K, Voloch CM, Serra-Freire NM, Machado-Ferreira E, Amorim M, Gazêta GS. Analysis of *Amblyomma sculptum* haplotypes in an area endemic for Brazilian spotted fever. Med Vet Entomol 2016;30:342–50. https://doi.org/10.1111/mve.12174.

[62] Casati S, Sager H, Gern L, Piffaretti J-C. Presence of potentially pathogenic Babesia sp. for human in Ixodes ricinus in Switzerland. Ann Agric Environ Med 2006;13:65–70.

[63] Da Silva FM, Noyes H, Campaner M, Junqueira ACV, Coura JR, Añez N, et al. Phylogeny, taxonomy and grouping of *Trypanosoma rangeli* isolates from man, triatomines and sylvatic mammals from widespread geographical origin based on SSU and ITS ribosomal sequences. Parasitology 2004;129:549–61. https://doi.org/10.1017/s0031182004005931.

[64] Ramírez JD, Duque MC, Montilla M, Cucunubá Z, Guhl F. Natural and emergent *Trypanosoma cruzi* I genotypes revealed by mitochondrial (Cytb) and nuclear (SSU rDNA) genetic markers. Experimental Parasitology 2012;132:487–94. https://doi.org/10.1016/j.exppara.2012.09.017.

[65] Regnery RL, Spruill CL, Plikaytis BD. Genotypic identification of rickettsiae and estimation of intraspecies sequence divergence for portions of two rickettsial genes. Journal of Bacteriology 1991;173:1576–89. https://doi.org/10.1128/jb.173.5.1576-1589.1991.

[66] Maggi RG, Diniz PP, Cadena MB, Breitschwerdt EB. The Use of Molecular Diagnostic Techniques to Detect *Anaplasma*, *Bartonella* and *Ehrlichia* Species in Arthropods or Patients. The International Canine Vector-Borne Disease Symposium, Billesley, Alcester, UK: 2006, p. 9–14.

[67] Maia C, Ramos C, Coimbra M, Bastos F, Martins A, Pinto P, et al. Bacterial and protozoal agents of feline vector-borne diseases in domestic and stray cats from southern Portugal. Parasit Vectors 2014;7:115. https://doi.org/10.1186/1756-3305-7-115.

[68] Heylen D, Tijsse E, Fonville M, Matthysen E, Sprong H. Transmission dynamics of *Borrelia burgdorferi* s.l. in a bird tick community. Environ Microbiol 2013;15:663–73. https://doi.org/10.1111/1462-2920.12059.

[69] Brown GK, Martin AR, Roberts TK, Aitken RJ. Detection of *Ehrlichia platys* in dogs in Australia. Aust Vet J 2001;79:554–8. https://doi.org/10.1111/j.1751-0813.2001.tb10747.x.

[70] Alberti A, Zobba R, Chessa B, Addis MF, Sparagano O, Pinna Parpaglia ML, et al. Equine and Canine *Anaplasma phagocytophilum* Strains Isolated on the Island of Sardinia (Italy) Are Phylogenetically Related to Pathogenic Strains from the United States. Applied and Environmental Microbiology 2005;71:6418–22. https://doi.org/10.1128/AEM.71.10.6418-6422.2005.

[71] Felsenstein J. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 1985;39:783–91. https://doi.org/10.1111/j.1558-5646.1985.tb00420.x.

[72] Saitou N, Nei M. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Molecular Biology and Evolution 1987;4:406–25. https://doi.org/10.1093/oxfordjournals.molbev.a040454.

[73] Nei M, Kumar S, Nei M, Kumar S. Molecular Evolution and Phylogenetics. Oxford, New York: Oxford University Press; 2000.

[74] Tamura K, Stecher G, Kumar S. MEGA11: molecular evolutionary genetics analysis version 11. Molecular Biology and Evolution 2021;38:3022–7.

[75] Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, et al. IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. Molecular Biology and Evolution 2020;37:1530–4. https://doi.org/10.1093/molbev/msaa015.

[76] Tamura K. Estimation of the number of nucleotide substitutions when there are strong transition-transversion and G+ C-content biases. Mol Biol Evol 1992;9:678–87.

[77] Tamura K, Nei M. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Molecular Biology and Evolution 1993;10:512–26.

[78] Reiczigel J, Marozzi M, Fábián I, Rózsa L. Biostatistics for Parasitologists – A Primer to Quantitative Parasitology. Trends in Parasitology 2019;35:277–81. https://doi.org/10.1016/j.pt.2019.01.003.

[79] R Core Team. R: A Language and Environment for Statistical Computing 2023.

[80] Sándor AD, Mărcuţan DI, D'Amico G, Gherman CM, Dumitrache MO, Mihalca AD. 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 2014;9:e89378. https://doi.org/10.1371/journal.pone.0089378.

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

[82] Norte AC, Ramos JA, Gern L, Núncio MS, Lopes de Carvalho I. 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 2013;15:386–97. https://doi.org/10.1111/j.1462-2920.2012.02834.x.

[83] Norte AC, de Carvalho IL, Ramos JA, Gonçalves M, Gern L, Núncio MS. Diversity and seasonal patterns of ticks parasitizing wild birds in western Portugal. Exp Appl Acarol 2012;58:327–39. https://doi.org/10.1007/s10493-012-9583-4.

[84] Rageau J. Répartition géographique et rôle pathogène des tiques (acariens: Argasidae et Ixodidae) en France. Wiadomości Parazytologiczne 1972;18.

[85] Tomassone L, Grego E, Auricchio D, Iori A, Giannini F, Rambozzi L. Lyme borreliosis spirochetes and spotted fever group rickettsiae in ixodid ticks from Pianosa island, Tuscany Archipelago, Italy. Vector Borne Zoonotic Dis 2013;13:84–91. https://doi.org/10.1089/vbz.2012.1046.

[86] Diakou A, Norte AC, Lopes de Carvalho I, Núncio S, Nováková M, Kautman M, et al. Ticks and tick-borne pathogens in wild birds in Greece. Parasitol Res 2016;115:2011–6. https://doi.org/10.1007/s00436-016-4943-3.

[87] Norte AC, Da Silva LP, Tenreiro PJQ, Felgueiras MS, Araújo PM, Lopes PB, et al. Patterns of tick infestation and their Borrelia burgdorferi sl infection in wild birds in Portugal. Ticks and Tick-Borne Diseases 2015;6:743–50.

[88] Llopis IV, Tomassone L, Grego E, Silvano F, Rossi L. Investigation into Usutu and West Nile viruses in ticks from wild birds in Northwestern Italy, 2012-2014. New Microbiol 2017;40:56–7.

[89] Mărcuţan I-D, Kalmár Z, Ionică AM, D'Amico G, Mihalca AD, Vasile C, et al. Spotted fever group rickettsiae in ticks of migratory birds in Romania. Parasit Vectors 2016;9:294. https://doi.org/10.1186/s13071-016-1565-7.

[90] Arthur DR, Thompson GB. LXXIX.—Records of ticks collected from birds in the British Isles. Journal of Natural History 1953;6:797–800.

[91] Jameson LJ, Medlock JM. Tick surveillance in Great Britain. Vector Borne Zoonotic Dis 2011;11:403–12. https://doi.org/10.1089/vbz.2010.0079.

[92] Siuda K, Majszyk A, Nowak M. Ticks (Acari: Ixodida) parasitizing birds (Aves) in Poland. Biol Lett 2006;43:147–51.

[93] Kristofěk J, MaSÁN P, Sustek Z, Kloubec B. Arthropods (Pseudoscorpionida, Acari, Coleóptera, Siphonaptera) in nests of the tengmalm's owl, *Aegolius funereus*. Biologia, Bratislava 2003;58:231–40.

[94] Spitalská E, Literák I, Kocianová E, Taragel'ová V. 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 2011;11:1235–41. https://doi.org/10.1089/vbz.2010.0210.

[95] Literak I, Kocianova E, Dusbabek F, Martinu J, Podzemny P, Sychra O. Winter infestation of wild birds by ticks and chiggers (Acari: Ixodidae, Trombiculidae) in the Czech Republic. Parasitol Res 2007;101:1709–11. https://doi.org/10.1007/s00436-007-0702-9.

[96] Martyn KP. Provisional atlas of the ticks (Ixodoidea) of the British Isles 1988.

[97] Jaenson TG, Tälleklint L, Lundqvist L, Olsen B, Chirico J, Mejlon H. Geographical distribution, host associations, and vector roles of ticks (Acari: Ixodidae, Argasidae) in Sweden. J Med Entomol 1994;31:240–56. https://doi.org/10.1093/jmedent/31.2.240.

[98] Novakova M, Bulkova A, Costa FB, Kristin A, Krist M, Krause F, et al. Molecular characterization of "Candidatus *Rickettsia vini*" in I*xodes arboricola* from the Czech Republic and Slovakia. Ticks Tick Borne Dis 2015;6:330–3. https://doi.org/10.1016/j.ttbdis.2015.02.006.

[99] Ferianc O, Lichard M. Birds in the Tribec and Hronský Inovec mountains as hosts of ticks. Bull World Health Organ 1967;36 Suppl:19–23.

[100] Papadopoulos B, Humair PF, Aeschlimann A, Vaucher C, Buttiker W. Ticks on birds in Switzerland. Acarologia 2002;42:3–19.

[101] Krčmar S. Hard ticks (Acari, Ixodidae) of Croatia. Zookeys 2012:19–57. https://doi.org/10.3897/zookeys.234.3658.

[102] Haarløv N. Variation in the ixodid tick, *Ixodes arboricola* Schulze & Schlottke 1929. Parasitology 1962;52:425–39.

[103] Petney TN, Pfäffle MP, Skuballa JD. An annotated checklist of the ticks (Acari: Ixodida) of Germany. Systematic and Applied Acarology 2012;17:115–70.

[104] Ciebiera O, Jerzak L, Nowak-Chmura M, Bocheński M. Ticks (Acari: Ixodida) on birds (Aves) migrating through the Polish Baltic coast. Exp Appl Acarol 2019;77:241–51. https://doi.org/10.1007/s10493-019-00341-z.

[105] Heylen DJA, Van Oosten AR, Devriendt N, Elst J, De Bruyn L, Matthysen E. Seasonal feeding activity of the tree-hole tick, *Ixodes arboricola*. Parasitology 2014;141:1044–51. https://doi.org/10.1017/S0031182014000225.

[106] Nowak-Chmura M, Siuda K, Wegner Z, Piksa K. Species diversity of ticks (Acari: Ixodida) on migrating birds on the Baltic Sea coast of Poland. Zool Stud 2012;51:7.

[107] Palomar AM, Portillo A, Crespo A, Santibáñez S, Mazuelas D, Oteo JA. Prevalence of "Candidatus *Rickettsia vini*" in *Ixodes arboricola* ticks in the North of Spain, 2011-2013. Parasit Vectors 2015;8:110. https://doi.org/10.1186/s13071-015-0724-6.

[108] Garben AFM, Lina PHC, Jansen J, Van Bronswijk J. Teken (Ixodida) van vogels gevangen te Meyendel (Gemeente's-Gravenhage). Entomologische Berichten 1978;38:156–8.

[109] Palomar AM, Santibáñez P, Mazuelas D, Roncero L, Santibáñez S, Portillo A, et al. Role of birds in dispersal of etiologic agents of tick-borne zoonoses, Spain, 2009. Emerg Infect Dis 2012;18:1188–91. https://doi.org/10.3201/eid1807.111777.

[110] Van Oosten AR, Heylen DJA, Matthysen E. Host specificity of a bird-specialised endophilic ectoparasite, the tree-hole tick *Ixodes arboricola*. Parasitol Res 2014;113:4397–405. https://doi.org/10.1007/s00436-014-4116-1.

[111] Cull B, Pietzsch ME, Hansford KM, Gillingham EL, Medlock JM. Surveillance of British ticks: An overview of species records, host associations, and new records of Ixodes ricinus distribution. Ticks Tick Borne Dis 2018;9:605–14. https://doi.org/10.1016/j.ttbdis.2018.01.011.

[112] Hornok S, Kováts D, Horváth G, Kontschán J, Farkas R. Checklist of the hard tick (Acari: Ixodidae) fauna of Hungary with emphasis on host-associations and the emergence of *Rhipicephalus sanguineus*. Exp Appl Acarol 2020;80:311–28. https://doi.org/10.1007/s10493-019-00461-6.

[113] Obsomer V, Wirtgen M, Linden A, Claerebout E, Heyman P, Heylen D, et al. 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. Parasit Vectors 2013;6:190. https://doi.org/10.1186/1756-3305-6-190.

[114] KriStofìk J, Masan P, Sustek Z, Gajdos P. Arthropods in the nests of penduline tit (*Remiz pendulinus*). BIOLOGIA-BRATISLAVA- 1993;48:493–493.

[115] Hasle G, Bjune G, Edvardsen E, Jakobsen C, Linnehol B, Røer JE, et al. Transport of ticks by migratory passerine birds to Norway. J Parasitol 2009;95:1342–51. https://doi.org/10.1645/GE-2146.1.

[116] Heylen DJA, Matthysen E. Contrasting detachment strategies in two congeneric ticks (Ixodidae) parasitizing the same songbird. Parasitology 2010;137:661–7. https://doi.org/10.1017/S0031182009991582.

[117] Siuda K, Szymański S. [A case of bringing along Mediterranean ticks *Ixodes (Ixodes) festai* Rondelli, 1926 (Acari: Ixodida: Ixodidae) to Poland by migrating birds]. Wiad Parazytol 1991;37:25–9.

[118] Nebogatkin IV. Birds as the feeders of ticks (Acari, Ixodida) in megalopolis of Kyiv. Вестник Зоологии 2014:467–70.

[119] Pietzsch ME, Mitchell R, Jameson LJ, Morgan C, Medlock JM, Collins D, et al. Preliminary evaluation of exotic tick species and exotic pathogens imported on migratory birds into the British Isles. Vet Parasitol 2008;155:328–32. https://doi.org/10.1016/j.vetpar.2008.05.006.

[120] Schilling F, Böttcher M, Walter G. Probleme des Zeckenbefalls bei Nestlingen des Wanderfalken (*Falco peregrinus*). Journal Für Ornithologie 1981;122:359–67.

[121] Sándor AD, Kalmár Z, Matei I, Ionică AM, Mărcuţan I-D. Urban Breeding Corvids as Disseminators of Ticks and Emerging Tick-Borne Pathogens. Vector Borne Zoonotic Dis 2017;17:152–4. https://doi.org/10.1089/vbz.2016.2054.

[122] Labbé Sandelin L, Tolf C, Larsson S, Wilhelmsson P, Salaneck E, Jaenson TGT, et al. Candidatus *Neoehrlichia mikurensis* in Ticks from Migrating Birds in Sweden. PLoS One 2015;10:e0133250. https://doi.org/10.1371/journal.pone.0133250.

[123] Dubska L, Literak I, Kocianova E, Taragelova V, Sverakova V, Sychra O, et al. Synanthropic birds influence the distribution of *Borrelia* species: analysis of *Ixodes ricinus* ticks feeding on passerine birds. Appl Environ Microbiol 2011;77:1115–7. https://doi.org/10.1128/AEM.02278-10.

[124] Guglielmone AA, Robbins RG, Apanaskevich DA, Petney TN, Estrada-Peña A, Horak IG. The Hard Ticks of the World: (Acari: Ixodida: Ixodidae). Springer Science & Business Media; 2013.

[125] Christensen ND, Skirnisson K, Nielsen ÓK. The Parasite Fauna of the Gyrfalcon (Falco rusticolus) in Iceland. J Wildl Dis 2015;51:929–33. https://doi.org/10.7589/2015-01-022.

[126] Jaenson TG, Jensen J. Records of ticks (Acari, Ixodidae) from the Faroe islands. Norwegian Journal of Entomology 2007;54:11.

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

[128] Klaus C, Gethmann J, Hoffmann B, Ziegler U, Heller M, Beer M. Tick infestation in birds and prevalence of pathogens in ticks collected from different places in Germany. Parasitol Res 2016;115:2729–40. https://doi.org/10.1007/s00436-016-5022-5.

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

[130] Toma L, De Liberato C, Magliano A, Montemaggiore A, Di Luca M, Mereu Piras P, Fois F. Recenti segnalazioni di Ixodes festai in Sardegna. Bollettino Dell'Associazione Romana Di Entomologia 2014;69:1–5.

[131] Osacar-Jimenez JJ, Estrada-Peña A, Lucientes-Curdi J. Ticks (Acarina: Ixodidae) of wild birds in the Ebro Middle basin (North-east Spain). Acarologia 1998;39:23–31.

[132] Chastel C, Guiguen C, Chastel O, Beaucournu JC. Pouvoir pathogène, rôle vecteur et hôtes nouveaux d'I*xodes pari* (= *I. frontalis*)(Acari; Ixodoidea; Ixodidae). Annales de Parasitologie Humaine et Comparée 1991;66:27–32.

[133] Doby JM. Contribution to the knowledge of Ixodes (Trichotoixodes) pari Leach (= I. frontalis (Panzer))(Acari: Ixodidae), a tick specific to birds. Acarologia 1999;39:315–25.

[134] Literak I, Norte AC, Núncio MS, de Carvalho IL, Ogrzewalska M, Nováková M, et al. Ticks on passerines from the Archipelago of the Azores as hosts of borreliae and rickettsiae. Ticks Tick Borne Dis 2015;6:607–10. https://doi.org/10.1016/j.ttbdis.2015.05.003.

[135] Heylen D, Fonville M, Docters van Leeuwen A, Stroo A, Duisterwinkel M, van Wieren S, et al. Pathogen communities of songbird-derived ticks in Europe's low countries. Parasit Vectors 2017;10:497. https://doi.org/10.1186/s13071-017-2423-y.

[136] Palomar AM, Portillo A, Santibáñez P, Mazuelas D, Roncero L, García-Álvarez L, et al. Detection of tick-borne *Anaplasma bovis, Anaplasma phagocytophilum* and *Anaplasma centrale* in Spain. Med Vet Entomol 2015;29:349–53. https://doi.org/10.1111/mve.12124.

[137] Palomar AM, Portillo A, Santibáñez P, Mazuelas D, Roncero L, Gutiérrez Ó, et al. Presence of Borrelia turdi and *Borrelia valaisiana* (Spirochaetales: Spirochaetaceae) in Ticks Removed From Birds in the North of Spain, 2009-2011. J Med Entomol 2017;54:243–6. https://doi.org/10.1093/jme/tjw158.

[138] Wilhelmsson P, Jaenson TGT, Olsen B, Waldenström J, Lindgren P-E. 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. Parasit Vectors 2020;13:607. https://doi.org/10.1186/s13071-020-04493-5.

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

[140] Thompson GB, Arthur DR. VI.—Records of ticks collected from birds in the British Isles.—2. Annals and Magazine of Natural History 1955;8:57–60.

[141] Thompson GB, Arthur DR. XLIV.—Records of ticks collected from birds in the British Isles.—3. Annals and Magazine of Natural History 1956;9:385–90.

[142] Homsher PJ, Sonenshine DE. Scanning electron microscopy of ticks for systematic studies. 2. Structure of Haller's organ in Ixodes brunneus and *Ixodes frontalis*. J Med Entomol 1977;14:93–7. https://doi.org/10.1093/jmedent/14.1.93.

[143] Mannelli A, Nebbia P, Tramuta C, Grego E, Tomassone L, Ainardi R, et al. Borrelia burgdorferi sensu lato infection in larval *Ixodes ricinus* (Acari: Ixodidae) feeding on blackbirds in northwestern Italy. J Med Entomol 2005;42:168–75. https://doi.org/10.1093/jmedent/42.2.168.

[144] Lommano E, Dvořák C, Vallotton L, Jenni L, Gern L. Tick-borne pathogens in ticks collected from breeding and migratory birds in Switzerland. Ticks Tick Borne Dis 2014;5:871–82. https://doi.org/10.1016/j.ttbdis.2014.07.001.

[145] Jameson LJ, Morgan PJ, Medlock JM, Watola G, Vaux AGC. Importation of *Hyalomma marginatum*, vector of Crimean-Congo haemorrhagic fever virus, into the United Kingdom by migratory birds. Ticks Tick Borne Dis 2012;3:95–9. https://doi.org/10.1016/j.ttbdis.2011.12.002.

[146] Cafiso A, Bazzocchi C, De Marco L, Opara MN, Sassera D, Plantard O. Molecular screening for Midichloria in hard and soft ticks reveals variable prevalence levels and bacterial loads in different tick species. Ticks Tick Borne Dis 2016;7:1186–92. https://doi.org/10.1016/j.ttbdis.2016.07.017.

[147] Marie-Angèle P, Lommano E, Humair P-F, Douet V, Rais O, Schaad M, et al. Prevalence of Borrelia burgdorferi sensu lato in ticks collected from migratory birds in Switzerland. Appl Environ Microbiol 2006;72:976–9. https://doi.org/10.1128/AEM.72.1.976-979.2006.

[148] Chastel C, Monnat JY, Le Lay G, Beaucournu JC. Syndrome neurologique mortel chez une tourterelle turque (*Streptopelia decaocto*) et fixation de la tique (I*xodes pari* (= *I. frontalis*). Annales de Parasitologie Humaine et Comparée 1981;56:349–51.

[149] Battisti E, Urach K, Hodžić A, Fusani L, Hufnagl P, Felsberger G, et al. Zoonotic Pathogens in Ticks from Migratory Birds, Italy. Emerg Infect Dis 2020;26:2986–8. https://doi.org/10.3201/eid2612.181686.

[150] Santos-Silva MM, Sousa R, Santos AS, Melo P, Encarnação V, Bacellar F. Ticks parasitizing wild birds in Portugal: detection of R*ickettsia aeschlimannii, R. helvetica* and *R. massiliae*. Exp Appl Acarol 2006;39:331–8. https://doi.org/10.1007/s10493-006-9008-3.

[151] Millán J, Gortazar C, Martín-Mateo MP, Villafuerte R. Comparative survey of the ectoparasite fauna of wild and farm-reared red-legged partridges (*Alectoris rufa*), with an ecological study in wild populations. Parasitol Res 2004;93:79–85. https://doi.org/10.1007/s00436-004-1113-9.

[152] Calvete C, Estrada R, Lucientes J, Estrada A. Ectoparasite ticks and chewing lice of red-legged partridge, *Alectoris rufa*, in Spain. Med Vet Entomol 2003;17:33–7. https://doi.org/10.1046/j.1365-2915.2003.00402.x.

[153] MOROZOV A, PROCA A. TICKS (ACARI, IXODIDAE) ON INDIGENOUS AND MIGRATORY BIRDS IN CHISHINAU. DESCRIEREA CIP A CAMEREI NAŢIONALE A CĂRŢII n.d.:47.

[154] Saratsiotis A. Etude morphologique et observations biologiques sur Ixodes gibbosus Nuttall, 1916. Annales de Parasitologie Humaine et Comparée 1970;45:661–75.

[155] Estrada Pena A, Lucientes Curdi J, Castillo Hernandez JA, Sanchez Acedo C, Galmes Femenias M. Alectoris rufa, nuevo hospedador para Ixodes ventalloi e *Ixodes (Pholeoixodes) hexagonus*, en España. Revista Iberica de Parasitología (1941) 1984;44:215–6.

[156] Matulaityte V, Paulauskas A, Bratchikov M, Radzijevskaja J. New record of *Rickettsia vini* in Ixodes lividus ticks from Lithuania. Ticks Tick Borne Dis 2020;11:101372. https://doi.org/10.1016/j.ttbdis.2020.101372.

[157] Matulaitytė V, Radzijevskaja J, Paulauskas A. First records of Ixodes lividus from sand martin (*Riparia riparia*) nests in Lithuania. J Vector Ecol 2017;42:264–70. https://doi.org/10.1111/jvec.12266.

[158] Movila A, Gatewood A, Toderas I, Duca M, Papero M, Uspenskaia I, et al. Prevalence of Borrelia burgdorferi sensu lato in *Ixodes ricinus* and *I. lividus* ticks collected from wild birds in the Republic of Moldova. International Journal of Medical Microbiology 2008;298:149–53.

[159] Müller J, Clupa W, Seelig K-J. Zum Vorkommen von *Ixodes lividus* Koch (syn. *I. plumbeus* Leach) auf Uferschwalben, *Riparia riparia* (L.), im Kreis Staßfurt. Hercynia-Ökologie Und Umwelt in Mitteleuropa 1975;12:320–4.

[160] Nováková M, Heneberg P, Heylen DJA, Medvecký M, Muñoz-Leal S, Šmajs D, et al. Isolated populations of *Ixodes lividus* ticks in the Czech Republic and Belgium host genetically homogeneous *Rickettsia vini*. Ticks Tick Borne Dis 2018;9:479–84. https://doi.org/10.1016/j.ttbdis.2017.12.018.

[161] Ulmanen I, Saikku P, Vikberg P, Sorjonen J. *Ixodes lividus* (Acari) in sand martin colonies in Fennoscandia. Oikos 1977:20–6.

[162] Graham RI, Mainwaring MC, Du Feu R. Detection of spotted fever group *Rickettsia* spp. from bird ticks in the U.K. Med Vet Entomol 2010;24:340–3. https://doi.org/10.1111/j.1365-2915.2010.00886.x.

[163] Alves M. Effects of ectoparasites on the sand martin *Riparia riparia* nestlings. Ibis 1997;139:494–6.

[164] Isabel LDC, Cláudia NA. First report of *Ixodes lividus* (Koch, 1844) in sand martins *Riparia riparia* in Portugal. Systematic and Applied Acarology 2020;25:1883–8.

[165] Szép T, Møller AP. Cost of parasitism and host immune defence in the sand martin *Riparia riparia*: a role for parent-offspring conflict? Oecologia 1999;119:9–15. https://doi.org/10.1007/s004420050755.

[166] Szép T, Møller AP. Exposure to ectoparasites increases within-brood variability in size and body mass in the sand martin. Oecologia 2000;125:201–7. https://doi.org/10.1007/s004420000447.

[167] Nowak-Chmura M, Siuda K. Ticks of Poland. Review of contemporary issues and latest research. Ann Parasitol 2012;58:125–55.

[168] Waldenström J, Lundkvist A, Falk KI, Garpmo U, Bergström S, Lindegren G, et al. Migrating birds and tickborne encephalitis virus. Emerg Infect Dis 2007;13:1215–8. https://doi.org/10.3201/eid1308.061416.

[169] Geller J, Nazarova L, Katargina O, Leivits A, Järvekülg L, Golovljova I. Tick-borne pathogens in ticks feeding on migratory passerines in Western part of Estonia. Vector Borne Zoonotic Dis 2013;13:443–8. https://doi.org/10.1089/vbz.2012.1054.

[170] Comstedt P, Bergström S, Olsen B, Garpmo U, Marjavaara L, Mejlon H, et al. Migratory passerine birds as reservoirs of Lyme borreliosis in Europe. Emerg Infect Dis 2006;12:1087–95. https://doi.org/10.3201/eid1207.060127.

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

[172] Baines D, Becker M, Hart S. Sheep tick *Ixodes ricinus* management on Welsh hill farms of designated conservation importance: implications for nationally declining birds. Med Vet Entomol 2019;33:352–9. https://doi.org/10.1111/mve.12368.

[173] Wodecka B, Rymaszewska A, Skotarczak B. Host and pathogen DNA identification in blood meals of nymphal *Ixodes ricinus* ticks from forest parks and rural forests of Poland. Exp Appl Acarol 2014;62:543–55. https://doi.org/10.1007/s10493-013-9763-x.

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

[175] Arthur DR. XXXV.—Ticks collected from birds in Sweden. Annals and Magazine of Natural History 1952;5:305–8.

[176] Hasle G, Leinaas HP, Røed KH, Øines Ø. Transport of Babesia venatorum-infected Ixodes ricinus to Norway by northward migrating passerine birds. Acta Vet Scand 2011;53:41. https://doi.org/10.1186/1751-0147-53-41.

[177] Paulauskas A, Rosef O, Galdikaite E, Radzijevskaja J. Infestation with *Ixodes ricinus* ticks on migrating passerine birds in Lithuania and Norway 2009.

[178] Radzijevskaja J, Rosef O, Matulaitytė V, Paulauskas A. Borrelia burgdorferi sensu lato genospecies in *Ixodes ricinus* ticks feeding on passerine birds in southern Norway. Biologija 2016;62.

[179] Alekseev AN, Dubinina HV, Semenov AV, Bolshakov CV. Evidence of ehrlichiosis agents found in ticks (Acari: Ixodidae) collected from migratory birds. J Med Entomol 2001;38:471–4. https://doi.org/10.1603/0022-2585-38.4.471.

[180] Humair P-F, Douet V, Morán Cadenas F, Schouls LM, Van De Pol I, Gern L. Molecular identification of bloodmeal source in Ixodes ricinus ticks using 12S rDNA as a genetic marker. J Med Entomol 2007;44:869–80. https://doi.org/10.1603/0022-2585(2007)44[869:miobsi]2.0.co;2.

[181] Humair PF, Turrian N, Aeschlimann A, Gern L. *Ixodes ricinus* immatures on birds in a focus of Lyme borreliosis. Folia Parasitol (Praha) 1993;40:237–42.

[182] James MC, Furness RW, Bowman AS, Forbes KJ, Gilbert L. 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 2011;153:293–302.

[183] Morán Cadenas F, Rais O, Humair P-F, Douet V, Moret J, Gern L. Identification of host bloodmeal source and *Borrelia burgdorferi* sensu lato in field-collected *Ixodes ricinus* ticks in Chaumont (Switzerland). J Med Entomol 2007;44:1109–17. https://doi.org/10.1603/0022-2585(2007)44[1109:iohbsa]2.0.co;2.

[184] Bjöersdorff A, Bergström S, Massung RF, Haemig PD, Olsen B. Ehrlichia-infected ticks on migrating birds. Emerg Infect Dis 2001;7:877–9. https://doi.org/10.3201/eid0705.017517.

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

[186] Biernat B, Stańczak J, Michalik J, Sikora B, Cieniuch S. *Rickettsia helvetica* and *R. monacensis* infections in immature *Ixodes ricinus* ticks derived from sylvatic passerine birds in west-central Poland. Parasitol Res 2016;115:3469–77. https://doi.org/10.1007/s00436-016-5110-6.

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

[188] Falchi A, Dantas-Torres F, Lorusso V, Malia E, Lia RP, Otranto D. Autochthonous and migratory birds as a dispersion source for *Ixodes ricinus* in southern Italy. Exp Appl Acarol 2012;58:167–74. https://doi.org/10.1007/s10493-012-9571-8.

[189] Franke J, Moldenhauer A, Hildebrandt A, Dorn W. Are birds reservoir hosts for *Borrelia afzelii*? Ticks Tick Borne Dis 2010;1:109–12. https://doi.org/10.1016/j.ttbdis.2010.03.001.

[190] Gryczyńska A, Welc-Falęciak R. Long-term study of the prevalence of *Borrelia burgdorferi* s.l. infection in ticks (*Ixodes ricinus*) feeding on blackbirds (*Turdus merula*) in NE Poland. Exp Appl Acarol 2016;70:381–94. https://doi.org/10.1007/s10493-016-0082-x.

[191] Hanincová K, Taragelová V, Koci J, Schäfer SM, Hails R, Ullmann AJ, et al. Association of *Borrelia garinii* and *B. valaisiana* with songbirds in Slovakia. Appl Environ Microbiol 2003;69:2825–30. https://doi.org/10.1128/AEM.69.5.2825-2830.2003.

[192] Hildebrandt A, Fritzsch J, Franke J, Sachse S, Dorn W, Straube E. Co-circulation of emerging tick-borne pathogens in Middle Germany. Vector Borne Zoonotic Dis 2011;11:533–7. https://doi.org/10.1089/vbz.2010.0048.

[193] Hubálek Z, Anderson JF, Halouzka J, Hájek V. Borreliae in immature *Ixodes ricinus* (Acari:Ixodidae) ticks parasitizing birds in the Czech Republic. J Med Entomol 1996;33:766–71. https://doi.org/10.1093/jmedent/33.5.766.

[194] Kazarina A, Japiņa K, Keišs O, Salmane I, Bandere D, Capligina V, et al. Detection of tick-borne encephalitis virus in *I. ricinus* ticks collected from autumn migratory birds in Latvia. Ticks Tick Borne Dis 2015;6:178–80. https://doi.org/10.1016/j.ttbdis.2014.11.011.

[195] Kipp S, Goedecke A, Dorn W, Wilske B, Fingerle V. Role of birds in Thuringia, Germany, in the natural cycle of *Borrelia burgdorferi* sensu lato, the Lyme disease spirochaete. Int J Med Microbiol 2006;296 Suppl 40:125–8. https://doi.org/10.1016/j.ijmm.2006.01.001.

[196] Klitgaard K, Højgaard J, Isbrand A, Madsen JJ, Thorup K, Bødker R. Screening for multiple tick-borne pathogens in *Ixodes ricinus* ticks from birds in Denmark during spring and autumn migration seasons. Ticks Tick Borne Dis 2019;10:546–52. https://doi.org/10.1016/j.ttbdis.2019.01.007.

[197] Marsot M, Henry P-Y, Vourc'h G, Gasqui P, Ferquel E, Laignel J, et al. 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 2012;42:781–8. https://doi.org/10.1016/j.ijpara.2012.05.010.

[198] Matuschka FR, Spielman A. Loss of Lyme disease spirochetes from *Ixodes ricinus* ticks feeding on European blackbirds. Exp Parasitol 1992;74:151–8. https://doi.org/10.1016/0014-4894(92)90042-9.

[199] Michalik J, Wodecka B, Skoracki M, Sikora B, Stańczak J. Prevalence of avian-associated *Borrelia burgdorferi* sl genospecies in *Ixodes ricinus* ticks collected from blackbirds (*Turdus merula*) and song thrushes (*T. philomelos*). International Journal of Medical Microbiology 2008;298:129–38.

[200] Pajoro M, Pistone D, Varotto Boccazzi I, Mereghetti V, Bandi C, Fabbi M, et al. Molecular screening for bacterial pathogens in ticks (*Ixodes ricinus*) collected on migratory birds captured in northern Italy 2018.

[201] Skotarczak B, Rymaszewska A, Wodecka B, Sawczuk M, Adamska M, Maciejewska A. PCR detection of granulocytic *Anaplasma* and *Babesia* in Ixodes ricinus ticks and birds in west-central Poland. Ann Agric Environ Med 2006;13:21–3.

[202] Spitalská E, Literák I, Sparagano OAE, Golovchenko M, Kocianová E. Ticks (Ixodidae) from passerine birds in the Carpathian region. Wien Klin Wochenschr 2006;118:759–64. https://doi.org/10.1007/s00508-006-0729-4.

[203] Tokarevich NK, Panferova YA, Freylikhman OA, Blinova OV, Medvedev SG, Mironov SV, et al. *Coxiella burnetii* in ticks and wild birds. Ticks Tick Borne Dis 2019;10:377–85. https://doi.org/10.1016/j.ttbdis.2018.11.020.

[204] Aleksandrova NI, Christova I, Dimitrov D, Marinov MP, Panayotova E, Trifonova I, et al. Records of ixodid ticks on wild birds in Bulgaria. PROBLEMS of Infectious and Parasitic Diseases 2021;49:35–9.

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

[206] Franke J, Fritzsch J, Tomaso H, Straube E, Dorn W, Hildebrandt A. Coexistence of pathogens in host-seeking and feeding ticks within a single natural habitat in Central Germany. Appl Environ Microbiol 2010;76:6829–36. https://doi.org/10.1128/AEM.01630-10.

[207] Hildebrandt A, Franke J, Meier F, Sachse S, Dorn W, Straube E. The potential role of migratory birds in transmission cycles of *Babesia* spp., *Anaplasma phagocytophilum*, and *Rickettsia* spp. Ticks Tick Borne Dis 2010;1:105–7. https://doi.org/10.1016/j.ttbdis.2009.12.003.

[208] Žėkienė A, Paulauskas A, Radzijevskaja J, Jusys V. Molecular investigation of tick-borne pathogens in ticks collected on migratory birds in Lithuania. Biologija 2011;57.

[209] Movila A, Reye AL, Dubinina HV, Tolstenkov OO, Toderas I, Hübschen JM, et al. 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 and Zoonotic Diseases 2011;11:89–91.

[210] Toderaş I, Alekseev N, Movilă A, Dubinina H, Şapoval A. Molecular identification of *Rickettsia japonica*, *Rickettsia helvetica* and *Babesia* sp. Eu1 in ticks collected from some birds species. Buletinul Academiei de Ştiinţe a Moldovei Ştiinţele Vieţii 2008;306:91–7.

[211] Dubska L, Literak I, Kverek P, Roubalova E, Kocianova E, Taragelova V. Tick-borne zoonotic pathogens in ticks feeding on the common nightingale including a novel strain of *Rickettsia* sp. Ticks Tick Borne Dis 2012;3:265–8. https://doi.org/10.1016/j.ttbdis.2012.06.001.

[212] Hajduskova E, Literak I, Papousek I, Costa FB, Novakova M, Labruna MB, et al. “Candidatus *Rickettsia mendelii*”, a novel basal group rickettsia detected in *Ixodes ricinus* ticks in the Czech Republic. Ticks Tick Borne Dis 2016;7:482–6. https://doi.org/10.1016/j.ttbdis.2016.02.004.

[213] Hoodless AN, Kurtenbach K, Nuttall PA, Randolph SE. Effects of tick *Ixodes ricinus* infestation on pheasant *Phasianus colchicus* breeding success and survival. Wildlife Biology 2003;9:171–8.

[214] Garben AF, Vos H, van Bronswijk JE. Hemaphysalis punctata Canestrini and Fanzago 1877, a tick of pastured seadunes on the island of Texel (The Netherlands). Acarologia 1982;23:19–25.

[215] Fain A, Vangeluwe D, Degreef M, Wauthy G. Observations on mites inhabiting nests of *Bubo bubo* (L.)(Strigiformes, Strigidae) in Belgium. Belgian Journal of Zoology 1993;123:3–3.

[216] Sándor AD, Milchev B, Takács N, Kontschán J, Szekeres S, Hornok S. Five ixodid tick species including two morphotypes of *Rhipicephalus turanicus* on nestlings of Eurasian eagle owl (*Bubo bubo*) from south-eastern Bulgaria. Parasit Vectors 2021;14:334. https://doi.org/10.1186/s13071-021-04832-0.

[217] Douglas DJ, Pearce-Higgins JW. Variation in ectoparasitic sheep tick Ixodes ricinus infestation on European Golden Plover chicks *Pluvialis apricaria* and implications for growth and survival. Bird Study 2019;66:92–102.

[218] Mancini F, Toma L, Ciervo A, Di Luca M, Faggioni G, Lista F, et al. Virus investigation in ticks from migratory birds in Italy. New Microbiol 2013;36:433–4.

[219] Walter G, Massa R. Ein Beitrag zur Ektoparasitenfauna der Zugvögel in Norditalien 1. Journal of Applied Entomology 1987;103:523–7.

[220] Gallizzi K. Parasite-induced Transgenerational Effects in the Great Tit (“ *Parus Major*”). PhD Thesis. Verlag nicht ermittelbar, 2007.

[221] Baines D, Taylor L. Can acaricide-impregnated leg bands fitted to female red grouse reduce sheep tick parasitization of chicks and increase chick survival? Med Vet Entomol 2016;30:360–4. https://doi.org/10.1111/mve.12185.

[222] Fletcher K, Baines D. The effects of acaricide treatment of sheep on red grouse *Lagopus lagopus scotica* tick burdens and productivity in a multi-host system. Med Vet Entomol 2018;32:235–43. https://doi.org/10.1111/mve.12282.

[223] Arthur DR. LXXXV.—The larva of *Ixodes rothschildi* Nuttall & Warburton, 1911. Annals and Magazine of Natural History 1955;8:711–2.

[224] Nuttall PA, Kelly TC, Carey D, Moss SR, Harrap KA. Mixed infections with tick-borne viruses in a seabird colony in Eire. Arch Virol 1984;79:35–44. https://doi.org/10.1007/BF01314301.

[225] Dietrich M, Beati L, Elguero E, Boulinier T, McCoy KD. Body size and shape evolution in host races of the tick *Ixodes uriae*. Biological Journal of the Linnean Society 2013;108:323–34.

[226] Gómez-Díaz E, Boulinier T, Sertour N, Cornet M, Ferquel E, McCoy KD. Genetic structure of marine *Borrelia garinii* and population admixture with the terrestrial cycle of Lyme borreliosis. Environ Microbiol 2011;13:2453–67. https://doi.org/10.1111/j.1462-2920.2011.02515.x.

[227] Kempf F, Boulinier T, De Meeûs T, Arnathau C, McCOY KD. Recent evolution of host-associated divergence in the seabird tick *Ixodes uriae*. Molecular Ecology 2009;18:4450–62.

[228] Duron O, Cremaschi J, McCoy KD. The high diversity and global distribution of the intracellular bacterium *Rickettsiella* in the polar seabird tick *Ixodes uriae*. Microbial Ecology 2016;71:761–70.

[229] Gylfe null, Olsen B, Strasevicius D, Marti Ras N, Weihe P, Noppa L, et al. Isolation of Lyme disease *Borrelia* from puffins (*Fratercula arctica*) and seabird ticks (*Ixodes uriae*) on the Faeroe Islands. J Clin Microbiol 1999;37:890–6. https://doi.org/10.1128/JCM.37.4.890-896.1999.

[230] Danchin E. The incidence of the tick parasite *Ixodes uriae* in Kittiwake *Rissa tridactyla* colonies in relation to the age of the colony, and a mechanism of infecting new colonies. Ibis 1992;134:134–41.

[231] Barton TR, Harris MP, Wanless S. Natural attachment duration of nymphs of the tick *Ixodes uriae* (Acari: Ixodidae) on kittiwake *Rissa tridactyla* nestlings. Experimental & Applied Acarology 1995;19:499–509.

[232] Boulinier T, Danchin E. Population trends in Kittiwake *Rissa tridactyla* colonies in relation to tick infestation. Ibis 1996;138:326–34.

[233] Chastel C, Monnat JY, Le Lay G, Guiguen C, Quillien MC, Beaucournu JC. Studies on bunyaviridae including Zaliv Terpeniya virus isolated fromIxodes uriae ticks (Acarina: Ixodidae) in Brittany, France. Archives of Virology 1981;70:357–66.

[234] McCoy KD, Boulinier T, Tirard C. Comparative host-parasite population structures: disentangling prospecting and dispersal in the black-legged kittiwake *Rissa tridactyla*. Mol Ecol 2005;14:2825–38. https://doi.org/10.1111/j.1365-294X.2005.02631.x.

[235] Finney SK, Elston DA. Natural attachment duration of adult female ticks Ixodes uriae (Acari: Ixodidae) on free-living adult black-legged kittiwakes *Rissa tridactyla*. Experimental & Applied Acarology 1999;23:765–9.

[236] McCoy KD, Boulinier T, Schjørring S, Michalakis Y. Local adaptation of the ectoparasite Ixodes uriae to its seabird host. Evolutionary Ecology Research 2002;4:441–56.

[237] Kristjánsson TÖ, Jónsson JE, Svavarsson J. Variation in nest composition and abundances of ectoparasites between nests in colonially breeding common eiders *Somateria mollissima*. Bird Study 2016;63:346–52.

[238] Elsterová J, Černỳ J, Müllerová J, Šíma R, Coulson SJ, Lorentzen E, et al. Search for tick-borne pathogens in the Svalbard Archipelago and Jan Mayen. Polar Research 2015;34:27466.

[239] Nunn MA, Barton TR, Wanless S, Hails RS, Harris MP, Nuttall PA. Tick-borne Great Island Virus: (II) Impact of age-related acquired immunity on transmission in a natural seabird host. Parasitology 2006;132:241–53. https://doi.org/10.1017/S0031182005008954.

[240] Olsén B, Jaenson TG, Noppa L, Bunikis J, Bergström S. A Lyme borreliosis cycle in seabirds and *Ixodes uriae* ticks. Nature 1993;362:340–2. https://doi.org/10.1038/362340a0.

[241] Coulson SJ, Lorentzen E, Strøm H, Gabrielsen GW. The parasitic tick *Ixodes uriae* (Acari: Ixodidae) on seabirds from Spitsbergen, Svalbard. Polar Research 2009;28:399–402.

[242] Descamps S. Winter temperature affects the prevalence of ticks in an Arctic seabird. PLoS One 2013;8:e65374. https://doi.org/10.1371/journal.pone.0065374.

[243] Duron O, Jourdain E, McCoy KD. Diversity and global distribution of the *Coxiella* intracellular bacterium in seabird ticks. Ticks Tick Borne Dis 2014;5:557–63. https://doi.org/10.1016/j.ttbdis.2014.04.003.

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

[245] Ioannou I, Chochlakis D, Kasinis N, Anayiotos P, Lyssandrou A, Papadopoulos B, et al. Carriage of Rickettsia spp., *Coxiella burnetii* and *Anaplasma* spp. by endemic and migratory wild birds and their ectoparasites in Cyprus. Clinical Microbiology and Infection 2009;15:158–60.

[246] Morel P-C. Présence en France d'*Ixodes festai* Rondelli, 1926. Annales de Parasitologie Humaine et Comparée 1959;34:549–51.

[247] Pascucci I, Di Domenico M, Capobianco Dondona G, Di Gennaro A, Polci A, Capobianco Dondona A, et al. 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 2019;10:101272. https://doi.org/10.1016/j.ttbdis.2019.101272.

[248] Krištofík J, Mašán P, Šustek Z. Arthropods (Pseudoscorpionidea, Acarina, Coleoptera, Siphonaptera) in nests of the bearded tit (*Panurus biarmicus*). Biologia 2007;62:749–55.

[249] Tovornik D, Cerný V. Finding of *Haemaphysalis erinacei erinacei* Pavesi, 1884 on birds in Yugoslavia. Folia Parasitol (Praha) 1974;21:282.

[250] Akimov IA, Nebogatkin IV. Distribution of Tick *Haemaphysalis punctata* (Acari, Ixodidae) in Ukraine. Вестник Зоологии 2012:365–70.

[251] Pérez-Eid C, Cabrita J. The larva and the nymph of *Hyalomma (Hyalomma) lusitanicum* Koch, 1844 (Acari: Ixodida): morphological description, habitats, hosts. Acarologia 2004;43:327–35.

[252] Aeschlimann A, Büttiker W. Importations de Tiques en Suisse (Acarina Ixodoidea). Bulletin de La Société Entomologique Suisse 1975;48:69–75.

[253] Hubálek Z, Sedláček P, Estrada-Peña A, Vojtíšek J, Rudolf I. First record of *Hyalomma rufipes* in the Czech Republic, with a review of relevant cases in other parts of Europe. Ticks Tick Borne Dis 2020;11:101421. https://doi.org/10.1016/j.ttbdis.2020.101421.

[254] Akimov IA, Nebogatkin IV. Distribution of the Ixodid Tick *Hyalomma marginatum* (Acari, Ixodidae) in Ukraine. Вестник Зоологии 2011.

[255] England ME, Phipps P, Medlock JM, Atkinson PM, Atkinson B, Hewson R, et al. *Hyalomma* ticks on northward migrating birds in southern Spain: Implications for the risk of entry of Crimean-Congo haemorrhagic fever virus to Great Britain. J Vector Ecol 2016;41:128–34. https://doi.org/10.1111/jvec.12204.

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

[257] Hoffman T, Lindeborg M, Barboutis C, Erciyas-Yavuz K, Evander M, Fransson T, et al. Alkhurma Hemorrhagic Fever Virus RNA in *Hyalomma rufipes* Ticks Infesting Migratory Birds, Europe and Asia Minor. Emerg Infect Dis 2018;24:879–82. https://doi.org/10.3201/eid2405.171369.

[258] Kolodziejek J, Marinov M, Kiss BJ, Alexe V, Nowotny N. 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 2014;9:e109905. https://doi.org/10.1371/journal.pone.0109905.

[259] Lindeborg M, Barboutis C, Ehrenborg C, Fransson T, Jaenson TGT, Lindgren P-E, et al. Migratory birds, ticks, and crimean-congo hemorrhagic fever virus. Emerg Infect Dis 2012;18:2095–7. https://doi.org/10.3201/eid1812.120718.

[260] Chisu V, Zobba R, Foxi C, Pisu D, Masala G, Alberti A. Molecular detection and groEL typing of *Rickettsia aeschlimannii* in Sardinian ticks. Parasitol Res 2016;115:3323–8. https://doi.org/10.1007/s00436-016-5091-5.

[261] Matsumoto K, Parola P, Brouqui P, Raoult D. *Rickettsia aeschlimannii* in *Hyalomma* ticks from Corsica. Eur J Clin Microbiol Infect Dis 2004;23:732–4. https://doi.org/10.1007/s10096-004-1190-9.

[262] Socolovschi C, Reynaud P, Kernif T, Raoult D, Parola P. Rickettsiae of spotted fever group, *Borrelia valaisiana*, and *Coxiella burnetii* in ticks on passerine birds and mammals from the Camargue in the south of France. Ticks Tick Borne Dis 2012;3:355–60. https://doi.org/10.1016/j.ttbdis.2012.10.019.

[263] Mancuso E, Toma L, Polci A, d'Alessio SG, Di Luca M, Orsini M, et al. Crimean-Congo Hemorrhagic Fever Virus Genome in Tick from Migratory Bird, Italy. Emerg Infect Dis 2019;25:1418–20. https://doi.org/10.3201/eid2507.181345.

[264] Brown G, Martin A, Roberts T, Aitken R. Detection of *Ehrlichia platys* in dogs in Australia. Australian Veterinary Journal 2001;79:554–8. https://doi.org/10.1111/j.1751-0813.2001.tb10747.x.

[265] Hornok S, Ágh N, Takács N, Kontschán J, Hofmann-Lehmann R. *Haematospirillum* and insect Wolbachia DNA in avian blood. Antonie Van Leeuwenhoek 2018;111:479–83. https://doi.org/10.1007/s10482-017-0961-0.

[266] Da Silva FM, Noyes H, Campaner M, Junqueira ACV, Coura JR, Añez N, et al. Phylogeny, taxonomy and grouping of *Trypanosoma rangeli* isolates from man, triatomines and sylvatic mammals from widespread geographical origin based on SSU and ITS ribosomal sequences. Parasitology 2004;129:549–61. https://doi.org/10.1017/s0031182004005931.

[267] Kurchatov VI. Translation from Russian of Kurchatov, VI (1939) Biological Peculiarity of the Tick *Hyalomma marginatum* Koch, Vector of Equine Piroplasmosis. Sovetsk. Vet., 16 (5): 45-46. 1939.

[268] Norte AC, de Carvalho IL, Ramos JA, Gonçalves M, Gern L, Núncio MS. Diversity and seasonal patterns of ticks parasitizing wild birds in western Portugal. Exp Appl Acarol 2012;58:327–39. https://doi.org/10.1007/s10493-012-9583-4.

[269] Rubel F, Brugger K, Walter M, Vogelgesang JR, Didyk YM, Fu S, et al. Geographical distribution, climate adaptation and vector competence of the Eurasian hard tick *Haemaphysalis concinna*. Ticks and Tick-Borne Diseases 2018;9:1080–9. https://doi.org/10.1016/j.ttbdis.2018.04.002.

[270] Nosek J. The ecology, bionomics and behaviour of *Haemaphysalis (Haemaphysalis) concinna* Tick. Z Parasitenk 1971;36:233–41. https://doi.org/10.1007/BF00348561.

[271] Hornok S, Horváth G, Jongejan F, Farkas R. Ixodid ticks on ruminants, with on-host initiated moulting (apolysis) of *Ixodes*, *Haemaphysalis* and *Dermacentor* larvae. Veterinary Parasitology 2012;187:350–3.

[272] Daniel M, Malỳ M, Danielová V, Kříž B, Nuttall P. Abiotic predictors and annual seasonal dynamics of *Ixodes ricinus*, the major disease vector of Central Europe. Parasites & Vectors 2015;8:1–12.

[273] Meng H, Xu S, Yu Z, Liu Z, Liu J, Yang X, et al. The life cycle and occurrence of *Haemaphysalis concinna* (Acari: Ixodidae) under field conditions. Ticks and Tick-Borne Diseases 2014;5:887–91.

[274] Reynolds C, Kontschán J, Takács N, Solymosi N, Sándor AD, Keve G, et al. Shift in the seasonality of ixodid ticks after a warm winter in an urban habitat with notes on morphotypes of *Ixodes ricinus* and data in support of cryptic species within Ixodes frontalis. Experimental and Applied Acarology 2022;88:127–38.

[275] Plantard O, Hoch T, Daveu R, Rispe C, Stachurski F, Boué F, et al. Where to find questing *Ixodes frontalis* ticks? Under bamboo bushes! Ticks and Tick-Borne Diseases 2021;12:101625. https://doi.org/10.1016/j.ttbdis.2020.101625.

[276] Estrada-Peña A, Mihalca AD, Petney TN. Ticks of Europe and North Africa: a guide to species identification. Cham: Springer; 2017.

[277] Capek M, Literak I, Kocianova E, Sychra O, Najer T, Trnka A, et al. Ticks of the *Hyalomma marginatum* complex transported by migratory birds into Central Europe. Ticks and Tick-Borne Diseases 2014;5:489–93.

[278] Akimov IA, Nebogatkin IV. Distribution of Ticks from the Genus *Dermacentor* (Acari, Ixodidae) in Ukraine. Вестник Зоологии 2011;45:35–40.

[279] Wilhelmsson P, Jaenson TGT, Olsen B, Waldenstrom J, Lindgren P-E. 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 2020;13:607. https://doi.org/10.1186/s13071-020-04493-5.

[280] Toma L, Mancuso E, d'Alessio SG, Menegon M, Spina F, Pascucci I, et al. Tick species from Africa by migratory birds: a 3-year study in Italy. Exp Appl Acarol 2021;83:147–64. https://doi.org/10.1007/s10493-020-00573-4.

[281] Buczek AM, Buczek W, Buczek A, Bartosik K. The potential role of migratory birds in the rapid spread of ticks and tick-borne pathogens in the changing climatic and environmental conditions in Europe. International Journal of Environmental Research and Public Health 2020;17:2117.

[282] Janisch M. A hazai kullancsfauna feltérképezése [Geographical distribution of tick species in Hungary]. Állattani Közlöny 1959;47:103–10.

[283] Magano SR, Els DA, Chown SL. Feeding patterns of immature stages of *Hyalomma truncatum* and *Hyalomma marginatum rufipes* on different hosts. Experimental & Applied Acarology 2000;24:301–13.

[284] Hornok S, Cutajar B, Takács N, Galea N, Attard D, Coleiro C, et al. On the way between Africa and Europe: Molecular taxonomy of ticks collected from birds in Malta. Ticks and Tick-Borne Diseases 2022;13:102001. https://doi.org/10.1016/j.ttbdis.2022.102001.

[285] Márquez FJ, Caruz A. Phylogeography of *Hyalomma* (*Euhyalomma*) *lusitanicum* (Acarina, Parasitiformes, Ixodidae) in Andalusia based on mitochondrial cytochrome oxidase I gene. Experimental and Applied Acarology 2021;85:49–61.

[286] Hornok S. Allochronic seasonal peak activities of *Dermacentor* and *Haemaphysalis* spp. under continental climate in Hungary. Veterinary Parasitology 2009;163:366–9.

[287] Hubálek Z, Halouzka J, Juricova Z. Host-seeking activity of ixodid ticks in relation to weather variables. Journal of Vector Ecology 2003;28:159–65.

[288] Pomerantsev BI. Ixodid Ticks (Ixodidae). American Institute of Biological Sciences; 1959.

[289] Hoogstraal H. African Ixodoidea. Vol. I. Ticks of the Sudan (with special reference to Equatoria Province and with Preliminary Reviews of the Genera *Boophilus*, *Margaropus*, and *Hyalomma*). US Navy 1956:479–90.

[290] Wallmenius K, Barboutis C, Fransson T, Jaenson TGT, Lindgren P-E, Nystrom F, et al. Spotted fever *Rickettsia* species in *Hyalomma* and Ixodes ticks infesting migratory birds in the European Mediterranean area. Parasites Vectors 2014;7:318. https://doi.org/10.1186/1756-3305-7-318.

[291] Kiros S, Awol N, Tsegaye Y, Hadush B. Hard Ticks of Camel in Southern Zone of Tigray, Northern Ethiopia. J Parasitol Vector Biol 2014;6:151–5. https://doi.org/10.5897/JPVB2014.0162.

[292] Kerario II, Muleya W, Chenyambuga S, Koski M, Hwang S-G, Simuunza M. Abundance and distribution of Ixodid tick species infesting cattle reared under traditional farming systems in Tanzania. African Journal of Agricultural Research 2017;12:286–99.

[293] Li Y, Luo J, Liu Z, Guan G, Gao J, Ma M, et al. Experimental transmission of *Theileria* sp. (China 1) infective for small ruminants by *Haemaphysalis longicornis* and *Haemaphysalis qinghaiensis*. Parasitol Res 2007;101:533–8. https://doi.org/10.1007/s00436-007-0509-8.

[294] Hornok S, Kartali K, Takács N, Hofmann-Lehmann R. Uneven seasonal distribution of *Babesia canis* and its two 18S rDNA genotypes in questing *Dermacentor reticulatus* ticks in urban habitats. Ticks and Tick-Borne Diseases 2016;7:694–7.

[295] Rar VA, Epikhina TI, Suntsova OV, Kozlova IV, Lisak OV, Pukhovskaya NM, et al. Genetic variability of *Babesia parasites* in *Haemaphysalis* spp. and *Ixodes persulcatus* ticks in the Baikal region and Far East of Russia. Infection, Genetics and Evolution 2014;28:270–5.

[296] Pitó A, Fedorov D, Brlík V, Kontschán J, Keve G, Sándor AD, et al. 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. Current Research in Parasitology & Vector-Borne Diseases 2024:100201. https://doi.org/10.1016/j.crpvbd.2024.100201.

[297] Ebani VV, Guardone L, Rocchigiani G, Bascherini A, Cagnoli G, Bertelloni F, et al. Molecular survey on the presence of arthropod-borne bacteria and protozoans in roe deer (*Capreolus capreolus*) and ticks from Central Italy. Acta Tropica 2022;233:106586.

[298] Hornok S, Szekeres S, Horváth G, Takács N, Bek\Ho K, Kontschán J, et al. Diversity of tick species and associated pathogens on peri-urban wild boars–first report of the zoonotic *Babesia* cf. *crassa* from Hungary. Ticks and Tick-Borne Diseases 2022;13:101936.

[299] Strasek-Smrdel K, Korva M, Pal E, Rajter M, Skvarc M, Avsic-Zupanc T. Case of *Babesia crassa*–like infection, Slovenia, 2014. Emerging Infectious Diseases 2020;26:1038.

[300] Herrmann C, Voordouw MJ, Gern L. Ixodes ricinus ticks infected with the causative agent of Lyme disease, *Borrelia burgdorferi* sensu lato, have higher energy reserves. Int J Parasitol 2013;43:477–83. https://doi.org/10.1016/j.ijpara.2012.12.010.

[301] Rachinsky A, Guerrero FD, Scoles GA. Proteomic profiling of *Rhipicephalus* (*Boophilus*) microplus midgut responses to infection with *Babesia bovis*. Veterinary Parasitology 2008;152:294–313.

[302] Nartshuk EP, Matyukhin AV, Red'kin YA. Association of the louse-flies of the genus *Ornithoctona* Speiser, 1902 (Diptera: Hippoboscidae) with birds and first record of *O. australasiae* (Fabricius, 1805) from the Russian Far East. Far Eastern Entomologist 2018:23–8.

[303] Reeves WK, Lloyd JE. Louse flies, keds, and bat flies (Hippoboscoidea). Medical and veterinary entomology, Elsevier; 2019, p. 421–38.

[304] Santolíková A, Brzoňová J, Čepička I, Svobodová M. Avian louse flies and their trypanosomes: new vectors, new lineages and host–parasite associations. Microorganisms 2022;10:584.

[305] Trilar T, Krčmar S. Contribution to the knowledge of louse flies of Croatia (Diptera: Hippoboscidae). Natura Croatica: Periodicum Musei Historiae Naturalis Croatici 2005;14:131–40.

[306] González MA, Hidalgo JC, Talabante C, Bernal I. Nuevos datos faunísticos e interacciones de moscas piojo (Diptera: Hippoboscidae) parasitando aves capturadas con redes japonesas en el Sistema Central (España). Graellsia 2023;79:e200–e200.

[307] Petersen FT, Meier R, Kutty SN, Wiegmann BM. The phylogeny and evolution of host choice in the Hippoboscoidea (Diptera) as reconstructed using four molecular markers. Molecular Phylogenetics and Evolution 2007;45:111–22. https://doi.org/10.1016/j.ympev.2007.04.023.

[308] Nirmala X, Hypša V, Žurovec M. Molecular phylogeny of Calyptratae (Diptera: Brachycera): the evolution of 18S and 16S ribosomal rDNAs in higher dipterans and their use in phylogenetic inference. Insect Molecular Biology 2001;10:475–85. https://doi.org/10.1046/j.0962-1075.2001.00286.x.

[309] Yatsuk AA, Triseleva TA, Narchuk EP, Matyukhin AV, Safonkin AF. Morphology of the wings and attachment apparatus in the evolution of the family Hippoboscidae (Diptera). Integr Zool 2023:1749-4877.12786. https://doi.org/10.1111/1749-4877.12786.

[310] Wawman DC. *Ornithomya biloba, Pseudolynchia garzettae* and *Pseudolynchia canariensis* (Diptera: Hippoboscidae): three new United Kingdom colonists and potential disease vectors. Medical Vet Entomology 2023:mve.12703. https://doi.org/10.1111/mve.12703.

[311] Szép T. Madarak monitorozása: Ökológiai és evolúciós folyamatok feltárásának lehetőségei [Monitoring birds: Possibilities for exploring ecological and evolutionary processes] 2007.

[312] Keve G, Csörgő T, Kováts D, Benke A, Bende AT, Ágoston H, et al. Contributions to our knowledge on avian louse flies (Hippoboscidae: Ornithomyinae) with the first European record of the African species *Ornithoctona laticornis*. Parasites & Vectors 2024;17:237. https://doi.org/10.1186/s13071-024-06303-8.

[313] Belli A, Sarr A, Rais O, Rego ROM, Voordouw MJ. Ticks infected via co-feeding transmission can transmit Lyme borreliosis to vertebrate hosts. Sci Rep 2017;7:5006. https://doi.org/10.1038/s41598-017-05231-1.

[314] Čisovská Bazsalovicsová E, Víchová B, Oboňa J, Radačovská A, Blažeková V, Králová-Hromadová I. Bird Louse Flies *Ornithomya* spp. (Diptera: Hippoboscidae) as Potential Vectors of Mammalian *Babesia* and Other Pathogens. Vector Borne Zoonotic Dis 2023;23:275–83. https://doi.org/10.1089/vbz.2022.0088.

[315] Oboňa J, Sychra O, Greš S, Heřman P, Manko P, Roháček J, et al. A revised annotated checklist of louse flies (Diptera, Hippoboscidae) from Slovakia. Zookeys 2019;862:129–52. https://doi.org/10.3897/zookeys.862.25992.

[316] Baráková I, Derdáková M, Carpi G, Rosso F, Collini M, Tagliapietra V, et al. Genetic and ecologic variability among *Anaplasma phagocytophilum* strains, northern Italy. Emerg Infect Dis 2014;20:1082–5. https://doi.org/10.3201/eid2006.131023.

[317] Lesiczka PM, Hrazdilová K, Majerová K, Fonville M, Sprong H, Hönig V, et al. The Role of Peridomestic Animals in the Eco-Epidemiology of *Anaplasma phagocytophilum*. Microb Ecol 2021;82:602–12. https://doi.org/10.1007/s00248-021-01704-z.

[318] Rouxel C, Etienne A, Arné P, Le Barzic C, Girault G, Boulouis H-J, et al. *Anaplasma phagocytophilum* in urban and peri-urban passerine birds in Ile-de-France. Ticks Tick Borne Dis 2024;15:102350. https://doi.org/10.1016/j.ttbdis.2024.102350.

[319] Wilhelmsson P, Lager M, Jaenson TGT, Waldenström J, Olsen B, Lindgren P-E. *Anaplasma phagocytophilum* in Ticks Blood-Feeding on Migratory Birds in Sweden. Microorganisms 2024;12:735. https://doi.org/10.3390/microorganisms12040735.

[320] Oh M-R, Moon K-H, Kim S-Y, Kim Y-G, Choi C-Y, Kang C-W, et al. Prevalence of *Anaplasma* sp. in Thrushes (Family Turdidae) in Jeju Island, Republic of Korea. Journal of Veterinary Clinics 2014;31:206–11.

[321] Jahfari S, Coipan EC, Fonville M, van Leeuwen AD, Hengeveld P, Heylen D, et al. Circulation of four *Anaplasma phagocytophilum* ecotypes in Europe. Parasites Vectors 2014;7:365. https://doi.org/10.1186/1756-3305-7-365.

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

[323] Brotánková A, Fialová M, Čepička I, Brzoňová J, Svobodová M. Trypanosomes of the *Trypanosoma theileri* Group: Phylogeny and New Potential Vectors. Microorganisms 2022;10:294. https://doi.org/10.3390/microorganisms10020294.

[324] Mullen GR, Durden LA. Medical and veterinary entomology. 3rd ed. London, United Kingdom: Academic press; 2019.

[325] Hornok S, Ágh N, Takács N, Kontschán J, Hofmann-Lehmann R. Haematospirillum and insect Wolbachia DNA in avian blood. Antonie van Leeuwenhoek 2018;111:479–83. https://doi.org/10.1007/s10482-017-0961-0.

[326] Humrighouse BW, Emery BD, Kelly AJ, Metcalfe MG, Mbizo J, McQuiston JR. *Haematospirillum jordaniae* gen. nov., sp. nov., isolated from human blood samples.

Antonie van Leeuwenhoek 2016;109:493–500. https://doi.org/10.1007/s10482-016-0654-0.

[327] Szewc AM, Humrighouse BW, Livingston K, Gulvik CA, Nicholson AC, McQuiston JR. Detection of an emerging pathogen: A real time qualitative pcr assay targeting *Haematospirillum jordaniae* for EDTA whole blood and plasma clinical specimens. Diagnostic Microbiology and Infectious Disease 2024;109:116310. https://doi.org/10.1016/j.diagmicrobio.2024.116310.

[328] Pal E, Štrumbelj I, Kišek TC, Kolenc M, Pirš M, Rus KR, et al. *Haematospirillum jordaniae* Cellulitis and Bacteremia. Emerg Infect Dis 2022;28:2116–9. https://doi.org/10.3201/eid2810.220326.

8. Publications of the Doctoral Research Findings

a) Publications Published or Accepted in Peer-Reviewed Scientific Journals with an Impact Factor

1. Keve, G., Sándor, A.D. and Hornok, S., 2022. Hard ticks (Acari: Ixodidae) associated with birds in Europe: Review of literature data. *Frontiers in Veterinary Science*, *9*, p.928756.
2. Keve, G., Csörgő, T., Kováts, D. and Hornok, S., 2024. Long term evaluation of factors influencing the association of ixodid ticks with birds in Central Europe, Hungary. *Scientific Reports*, *14*(1), p.4958.
3. Keve, G., Csörgő, T., Benke, A., Huber, A., Mórocz, A., Németh, Á., Kalocsa, B., Tamás, E.A., Gyurácz, J., Kiss, O. and Kováts, D., 2023. Ornithological and molecular evidence of a reproducing *Hyalomma rufipes* population under continental climate in Europe. *Frontiers in Veterinary Science*, *10*, p.1147186.
4. Keve, G., Reynolds, C., Takács, N. and Hornok, S., 2025. Uneven temporal distribution of piroplasms (Piroplasmida: Babesiidae, Theileriidae) in *Haemaphysalis concinna* in an urban biotope of the Western Palearctic focus region of this tick species. *Ticks and Tick-borne Diseases*, *16*(2), p.102458.
5. Keve, G., Csörgő, T., Kováts, D., Benke, A., Bende, A.T., Ágoston, H., Mórocz, A., Németh, Á., Tamás, E.A., Huber, A. and Gyurácz, J., 2024. Contributions to our knowledge on avian louse flies (Hippoboscidae: Ornithomyinae) with the first European record of the African species *Ornithoctona laticornis*. *Parasites & Vectors*, *17*(1), p.237.

d) Conference presentations

1. Keve, G., Csörgő, T., Benke, A., Huber, A., Mórocz, A., Németh, Á., Kalocsa, B., Tamás, E.A., Gyurácz, J., Kiss, O., Kováts, D., Sándor, D.A., Karcza, Z. & Hornok, S., 2023. *Egy Hyalomma rufipes populáció jelenlétének ornitológiai bizonyítékai a Kárpát-medencében* [Ornithological evidence for the presence of a *Hyalomma rufipes* population in the Carpathian Basin] Presented in Hungarian at: Akadémiai Beszámolók, 30–31 January 2023.
2. Keve, G., Csörgő, T., Kováts, D., Benke, A., Bende, A., Ágoston, H., Mórocz, A., Németh, Á., Tamás, E.A., Huber, A., Gyurácz, J., Keve, G., Kontschán, J., Németh, A. & Hornok, S., 2024. *Madárkullancslegyek (Ornithomyinae) vizsgálata és egy afrikai fajuk (Ornithoctona laticornis) első európai megjelenése* [Study of Bird Louse Flies (Ornithomyinae) and the First European Occurrence of an African Species (*Ornithoctona laticornis*)]. Presented in Hungarian at: Akadémiai Beszámolók, 29–31 January 2024.

3. Keve, G., Reynolds, C., Takács, N. & Hornok, S., 2025. *Egy városi Haemaphysalis concinna populációban talált piroplazmák (Piroplasmida: Babesiidae, Theileriidae) egyenlőtlen időbeli eloszlása* [Uneven Temporal Distribution of Piroplasms (Piroplasmida: Babesiidae, Theileriidae) in an Urban Haemaphysalis concinna Population]. Presented in Hungarian at: Akadémiai Beszámolók, 20–22 January 2025.
4. Keve, G., Hornok, S., 2025. *A hazai madárkullancslégy állomány és az általuk közvetített kórokozók vizsgálata* [Study on the Hungarian Bird Louse Fly Population and the Pathogens They Transmit]. Presented in Hungarian at: Intézményi EKÖP Konferencia, 13 May 2025.
5. Keve, G., Csörgő, T., Benke, A., Huber, A., Mórocz, A., Németh, Á., Kalocsa, B., Tamás, E.A., Gyurácz, J., Kiss, O., Kováts, D., Sándor, A.D., Karcza, Z. & Hornok, S., 2023. *Ornithological and molecular evidence of a reproducing Hyalomma rufipes population under continental climate Europe*. Poster presented at: 15th International Symposium on Ticks and Tick-borne Diseases (ISTTBD-XV), 2023.
6. Keve, G. & Hornok, S., 2024. *The role of birds in the dispersal of ticks and other arthropod vectors*. Poster presented at: 11th Ticks and Tick-Borne Pathogens Conference (TTP11), 1–6 September 2024, Havana & Varadero, Cuba.

9. Supplementary Material

Supplementary materials are available as separate files.

List of supplementary materials:

Supplementary Table 1. List of bird host species and tick-occurrence cases extracted from publications. Bird species in red are rare vagrants or captive populations, they do not occur regularly in Europe.

Supplementary Figure 1. Reported occurrence of tick species according to avian orders. The number of bird species within an avian order, from which the relevant tick species was reported is encircled next to the name of avian order, along the line which connects it to the relevant tick species. Grouping of tick species according to habit preference, and of avian orders according to habitat type, nocturnal activity (inverse characters) and typical feeding level is simplified according to predominant traits of species in Europe.

Supplementary Table 2. List of HURING codes, as well as information on the migration habit, habitat type, feeding place and weight of the birds (if relevant for statistics).

Supplementary Figure 2. Temporal distribution of *Ixodes ricinus* and *Haemaphysalis concinna* in each year between 2014 and 2022

Supplementary Table 3. Bird species according to their migration habits, with the total number of ticks found on them

Supplementary Tabe 4. Avian host species that were found tick-infested in this study, shown according to collection site and spring or autumn migration intervals (the former including nesting period). The number of tick-infested birds sampled at the same location is shown in parentheses after the abbreviation of bird species name. Color code: red - long distance migrant, purple - resident or short/mid-distance migrant, blue - resident.

Supplementary Table 5. Avian host species that were found tick-infested in this study, shown according to collection site and spring or autumn migration intervals (the former including nesting period).

Supplementary Figure 3. The average annual precipitation (https://www.met.hu/) and temperature (https://www.mozaweb.com/search?search_=_középhomérséklet) in January in Hungary, based on data from the Hungarian Meteorological Service (OMSZ). The site of the discovered *Hyalomma rufipes* population is marked with a star.

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