



# Bidirectional tick transport by migratory birds of the African-Western Palearctic flyway over Turkish Thrace: observation of the current situation and future projection

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## Abstract

This study was carried out at a vital stopover site of migrating birds in the Turkish Thrace, European part of Turkey, on the Mediterranean/Black Sea Flyway. Ticks were collected from the birds captured in the four migration periods, i.e., autumn 2020, spring 2021, autumn 2021, and spring 2022, and identified morphologically. Throughout the study, 10,651 birds from 77 species were examined, and 671 belonging to 34 species were found infested. The infestation prevalence in total birds and the mean number of ticks per infested bird were 6.3% and 3.8 (range: 1–142), respectively. A total of 2573 ticks were collected with the following species distribution and numbers: *Ixodes* spp. 70 larvae, *I. frontalis* 1829 larvae, 337 nymphs, and 30 adults, *I. acuminatus* 16 nymphs and 42 adults, *I. ricinus* 39 larvae, 141 nymphs, and one adult, *Hyalomma* spp. seven larvae and 60 nymphs, and *Haemaphysalis* sp. one larva. Prevalence, intensity, and species distribution of the ticks in birds varied depending on the month, season, year, and species-specific migration phenology of the birds. The results show that precise determination of the tick-borne risk associated with migratory birds for a particular region necessarily requires long-term and comprehensive studies and indicates that anthropogenic climate change and habitat degradation can significantly differentiate the risk by influencing the migration phenology in birds and by making new regions suitable for the establishment of different ticks.

**Keywords** *Hyalomma rufipes* · Mediterranean/Black Sea Flyway · Migrating birds · Season · Tick dispersal · Tick infestation

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## Introduction

Hard ticks (Acari: Ixodida: Ixodidae) are ubiquitous hematophagous ectoparasites that transmit numerous viral, bacterial, and protozoan agents to humans and animals. The life cycle includes eggs, immature stages (larva and nymph), and adults. For the continuity of the biological process, the mature and immature stages suck blood from an animal host for a certain period (Sonenshine and Roe 2013). The preferences of tick species, and sometimes even biological stages of the same species, may differ in terms of ambient temperature, humidity, habitat condition, vegetation, and host species. While some species are highly host-specific, others can feed on different animals, and this selectivity is generally lower in immature stages compared to adults (Sonenshine and Roe 2013). This species-specific difference in ticks affects the distribution and density of ticks worldwide. However, the availability of the host is an indispensable condition for the establishment and persistence of ticks in a territory that applies to

all species. Besides, ticks, particularly in immature stages, have relatively weak dispersion ability and mostly cannot move more than a few meters. Thus, a host's reachability is as critical as its availability (Kar and Gargili Keles 2021).

All these factors indicated above put birds in a particular position in the biology, ecology, and epidemiology of ticks and tick-borne diseases, as they can be the host for many tick species, can transport ticks over short or long distances, even between continents, and can be the source of several tick-borne agents, some of which are zoonotic (Olsén et al. 1995; Diakou et al. 2016; Klitgaard et al. 2019; Wilhelmsson et al. 2020; Gray et al. 2021; Wimbauer et al. 2022). The emergence or geographical distribution of some vector-borne pathogens can be associated with birds, e.g., the tick-borne agent Crimean-Congo hemorrhagic fever virus (CCHF) (Bente et al. 2013) and the mosquito-borne agent West Nile virus (Hacioglu et al. 2017). To date, several agents have been detected in the ticks collected from the birds, such as *Borrelia burgdorferi* s.s., *Borrelia valaisiana*, *B. afzelii*, *B. garinii*, *B. turdi*, *Anaplasma phagocytophilum*, *Rickettsia helvetica*, *R. aeschlimannii*, *R. africae*, *Babesia divergens*, *Ba. microti*, *Ba. venatorum*, *Coxiella burnetii*, and Crimean Congo hemorrhagic fever virus (Kaiser et al. 1974; Ioannou et al. 2009; Hasle et al. 2011; Geller et al. 2013; Capligina et al. 2014; Grandi et al. 2020; Rollins et al. 2021; Uiterwijk et al. 2021).

The arrival of a new tick species and the pathogens they carry in a new area does not guarantee establishment or emergence (Gray et al. 2021). At this point, incompatibility in the local environmental conditions, such as climate, can be a significant obstacle. However, it is known that although the contemporary climate and environmental changes may strengthen this barrier for some tick species, they may weaken it for others (Kar and Gargili Keles 2021). For example, the change in the climate character in the Western Palearctic is predicted to shift in the south-north direction (Pontes et al. 2020), and such a shift is predicted to result in the northern invasion of some tropical tick species and tick-borne agents (Buczek et al. 2020). It has been pointed out that the African-Western Palearctic flyway, which is used by billions of birds carrying millions of ticks between the Afrotropical region and Europe annually, could play a critical role in this expansion in the future (Olsén et al. 1995; Hahn et al. 2009).

Studies on ticks in migratory birds have increased in the last decades as the importance of the subject has been better realized over time. However, the dynamics between migratory birds, tick species, and tick-borne agents still need to be fully elucidated. Besides, under the influence of ever-increasing environmental and climate change, it seems that the migratory characteristics of birds (Charmantier and Gienapp 2014; Pavon-Jordan et al. 2015), the phenology of tick species, and therefore all the relevant dynamics will

change dramatically (Kar and Gargili Keles 2021). For all these reasons, the importance of continuous monitoring of migrating birds needs to be emphasized (Toma et al. 2021).

This study was carried out at a crucial stopover site of migrating birds in Turkish Thrace, the European part of Turkey, on the Mediterranean/Black Sea (MBS) flyway, which is one of the longest and largest routes of the African-Western Palearctic flyways. Thrace is located approximately amidst Old World continents and is one of the most critical bottlenecks on the MBS. Birds passing through Thrace can travel one of the longest routes in the world, extending between South Africa, Madagascar, Rift Valley, The Nile Delta, the Middle East, Anatolia, Thrace, Europe, the north side of the Black Sea, and Scandinavia (Hahn et al. 2009; Najdenski et al. 2018). In Thrace, it is possible to see more than 350 bird species within a year, close to 300 of which are migratory. More than 100 species can use the region as a wintering ground (non-breeding area), and about 75 species as a breeding ground in summer. Around 150 species migrate between Europe and Africa, and over 60% go to sub-Saharan Africa for wintering. Millions of birds from sub-Saharan Africa pass through Thrace every year and head to Europe, around half of which are Passeriformes (Kirwan et al. 2008).

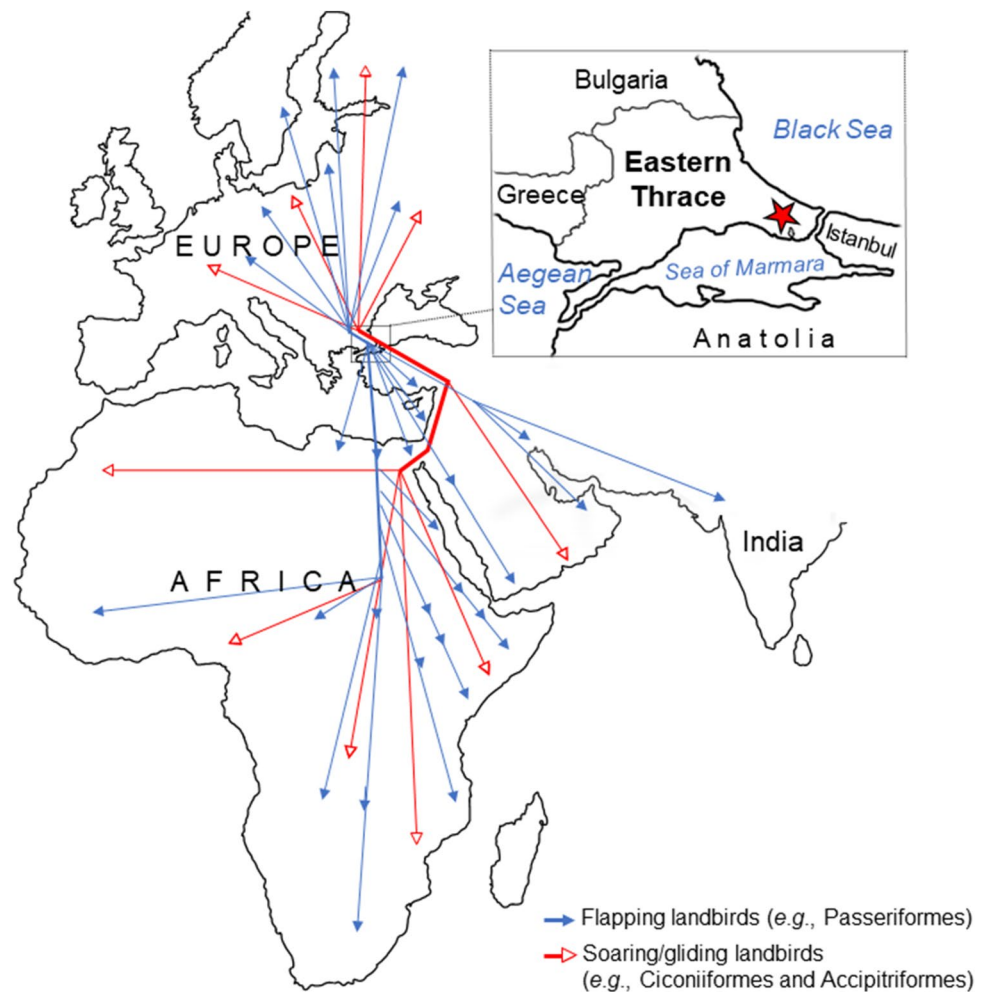
This study examined the mist-netted birds for the presence of ticks for 2 years, both spring and autumn migration periods. The records were evaluated regarding bird species, ticks, seasonality of the infestation, and relevant geographical and ecological drivers. The results were discussed within the frame of the current risk and possible future differentiation in this risk under the influence of anthropogenic climate change and ongoing differentiation or destruction of bird's and tick's habitats.

## Material and methods

### Study area

This study was carried out at a stopover site of migrating birds in the eastern tip of the Balkan Peninsula in Turkish Thrace, which is bordered by Greece, Bulgaria, the Bosphorus, the Black Sea, the Aegean Sea, and the Sea of Marmara (Fig. 1). The study site is located on the bank of Lake Kucukcekmece (40° 59' N, 28° 43' E), which has a length of 10 km, a surface area of 16 km<sup>2</sup>, and a depth of up to 20 m. This freshwater lake is in the south of Eastern Thrace, on the northern coast of the Sea of Marmara, and is separated from the sea by a sandbank. Although the lake is surrounded mainly by the urban of Istanbul, there are woodlands, parks, and grasslands on its shore, the width of which does not exceed 1.5 km. Lake Kucukcekmece, one of Thrace's important stopover sites, is heavily used by migratory passerine birds, particularly just crossing the Sea of Marmara.

**Fig. 1** Most probable migration routes of the landbirds passing through Turkish Thrace



### Bird captures and tick collection

The study was carried out with the approval of the General Directorate of Nature Conservation and National Parks, Ministry of Agriculture and Forestry, Republic of Turkey (protocol number 26137614-280.01.01-E.2141100 12.07.2019). Birds were captured with mist nets by experienced ringers during the following four main bird migration periods within the spring and autumn migration seasons: August 15–November 07, 2020; March 01–June 07, 2021; September 15–November 13, 2021, and March 22–June 06, 2022. Mist-netted birds were identified at the species level, ringed according to standard procedures, and examined in detail for the presence of ticks. Encountered ticks were removed using fine tweezers and taken to tubes individually per bird. The tubes, each labeled with the host species, ring numbers, and date, were stored at  $-20^{\circ}\text{C}$ . The ticks were identified at the species level under a stereomicroscope using the morphological keys (Estrada-Peña et al. 2017; Horak et al. 2018). The engorged nymphs of *Hyalomma* spp. collected during the spring migration seasons were taken individually

into sterile tubes. The tubes were incubated with total exposure to the local climatic conditions of the study area, out of direct sunlight and rain, and the molting and activation processes of the ticks were recorded.

### Classification of bird migration categories

The captured bird species were subjected to a broad classification following similar approaches described previously (Wilhelmsson et al. 2020), reflecting the characteristics of the Thracian populations. In this classification, the following parameters were considered: (i) the migration distances, (ii) the wintering areas of birds, and (iii) the differences between the Western Palearctic and the Afrotropical realm in terms of the species and population diversities of ticks (Estrada-Peña et al. 2017; Horak et al. 2018). Accordingly, the birds were classified into residents (R), short-distance migrants (S), medium-distance migrants (M), and long-distance migrants (L). The residents show local dispersal or no migration, and the others use different parts of Europe as breeding grounds. Of these, short-distance migrants mainly

winter in Anatolia, the Mediterranean coast of Turkey, and the Aegean islands. The medium-distance migrants winter in the Levant, North Africa, Mesopotamia, and The Persian Gulf. The vast majority of the long-distance migrants winter in sub-Saharan Africa, the others in the Indian Ocean coasts of the Middle East, the distal parts of the Red Sea basin, and a few species in Pakistan and India. In some bird species, different populations may follow different migration patterns (Busse 2000; Bairlein and Bonan 2018), and in such cases, all the possible categories were indicated for those species.

## Statistical analysis

Considering the bird ringing years (2020 autumn and 2021 spring–2021 autumn and 2022 spring) and seasons (2020 and 2021 autumn–2021 and 2022 spring), both the infestation status of bird species and the infestation characteristics of tick species on birds were tested statistically. Tick infestation intensities were used as the test data. While choosing the test statistic, whether the data were normally distributed or not was analyzed with the Kolmogorov–Smirnov test and the Shapiro–Wilk test, and it was decided that the test to be applied would be parametric or non-parametric, according to the result. The relations between all seasons were analyzed with the Kruskal–Wallis test, and the bilateral relations between the seasons and the ringing years were analyzed with the Mann–Whitney *U* test. The areas where birds are mostly found during feeding were grouped as mostly ground and mostly non-ground (trees or bushes), and the relationship between these parameters and tick infestation prevalence was analyzed with the Mann–Whitney *U* test. All statistical tests were performed with the IBM SPSS Statistics (24.0) program.

## Results

Throughout the study, 10651 birds belonging to 77 species from 46 genera in nine orders were examined for ticks. The Passeriformes (36 genera, 66 species, 10534 birds) constituted the most of the samples (98.9%). Ticks were found on 34 bird species from the following genera (abbreviations used in the text and tables): *Caprimulgus* (*Ca.*) from Caprimulgiformes order, *Otus* (*O.*) from Strigiformes order, *Jynx* (*J.*) and *Dendrocopos* (*D.*) from Piciformes order, and *Acrocephalus* (*Ac.*), *Anthus* (*An.*), *Cettia* (*Ce.*), *Curruca* (*Cu.*), *Cyanistes* (*Cy.*), *Erithacus* (*E.*), *Ficedula* (*Fi.*), *Fringilla* (*Fr.*), *Iduna* (*I.*), *Locustella* (*Lo.*), *Luscihana* (*Lu.*), *Muscicapa* (*M.*), *Parus* (*Pa.*), *Phoenicurus* (*Pho.*), *Phylloscopus* (*Phy.*), *Prunella* (*Pu.*), *Sylvia* (*S.*), *Troglodytes* (*Tr.*), and *Turdus* (*Tu.*) from Passeriformes order. No ticks were found on 835 birds belonging to 43 species from 32 genera in the orders Passeriformes

(26 genera, 37 species), Coraciiformes (1 genus, 1 species), Gruiformes (1 genus, 1 species), Bucerotiformes (1 genus, 1 species), Galliformes (1 genus, 1 species), and Accipitriformes (1 genus, 2 species). The records on the migration categories of birds showed that all or some populations of 4827 (45.3%) birds belonged to 28 species (36.4%) were resident (R), all or some populations of 6552 (61.5%) birds belonged to 51 (66.2%) species were long-distance migrants (L). The other birds were short (S) and/or medium-distance (M) migrants. Of the long-distance migrants, 44 species are known to go to sub-Saharan Africa for wintering, and nine species can overwinter in Africa or as far as Pakistan–India, depending on the populations passing through Turkey (Supplementary file 1, Fig. 1).

Ticks were found on 671 individuals belonging to 34 bird species. The prevalence of tick infestation (number of infested birds/total birds examined) was 6.3% in all birds examined (no. 10651). This value was 3.9 (110/2830), 6.6 (191/2879), 9.4 (290/3096), and 4.3 (80/1846) in the periods of autumn 2020, spring 2021, autumn 2021, and spring 2022, respectively. Mean tick intensity (mean number of ticks per infested bird) ( $\pm$ SD) was  $3.8 \pm 8.7$  (range: 1–142) in total, and this was  $2.3 \pm 6.8$  (1–68),  $2.1 \pm 3.1$  (1–39),  $5.7 \pm 11.8$  (1–142), and  $3.4 \pm 4.1$  (1–22) in the four seasons studied, respectively (Table 1). The highest prevalence was determined on *Tu. merula* with a value of 41.4% (126/305), and this species was followed by *E. rubecula* with a value of 14.9 (349/2349). The highest intensity was seen in October 2021 in an individual of *Tu. merula* with 142 ticks (140 larvae and two adult ticks).

Pairwise comparisons of bird species by mean tick infestation intensity between seasons and between ringing seasons were made statistically. In addition, all seasons within 2 years were statistically evaluated. Accordingly, a statistically significant relationship was found between infestation densities in the 2020 autumn and 2021 autumn seasons ( $p=0.045$ ), 2021 spring and 2021 autumn seasons ( $p=0.03$ ), and 2021 autumn and 2022 spring seasons ( $p=0.039$ ). In addition, the difference in mean infestation intensities between all autumn seasons and all spring seasons within 2 years was again shown to be in a statistically significant relationship ( $p=0.026$ ). Finally, we see a statistically significant result when comparing the mean infestation intensities observed in all seasons within two bird-ringing years ( $p=0.028$ ). When the infestation densities of tick species on all bird species were evaluated statistically by seasons, bird ringing years, autumn and spring seasons in 2 years, and all seasons within two bird ringing years, no statistical significance was observed between them (Table 2). The analysis did not reveal any significant relationship between the areas (ground and non-ground) used mainly by the birds during feeding and tick infestation prevalences ( $p=0.463$ ).

**Table 1** Seasonal characteristics of tick prevalence (no. of infested birds/no. of examined birds) and mean tick intensity (mean no. of ticks per infested bird) in birds

Bird species	Autumn 2020		Spring 2021	
	Prevalence	Mean intensity $\pm$ SD (range)	Prevalence	Mean intensity $\pm$ SD (range)
<i>Ac. palustris</i>	0 (0/32)	-	11.4 (4/35)	1.8 $\pm$ 1.0 (1–3)
<i>Ac. schoenobaenus</i>	0 (0/11)	-	50.0 (2/4)	1.5 $\pm$ 0.7 (1–2)
<i>Ac. scirpaceus</i>	0 (0/11)	-	0 (0/43)	-
<i>An. trivialis</i>	0 (0/2)	-	7.7 (1/13)	1
<i>Ca. europaeus</i>	0 (0/8)	-	0 (0/5)	-
<i>Ce. cetti</i>	0 (0/79)	-	8.5 (5/59)	1.6 $\pm$ 1.3 (1–4)
<i>Cu. communis</i>	0 (0/82)	-	10.7 (6/56)	2.0 $\pm$ 2.5 (1–7)
<i>Cu. curruca</i>	0 (0/77)	-	0.9 (1/116)	2.0
<i>Cu. melanocephala</i>	0 (0/51)	-	2.4 (2/83)	1.5 $\pm$ 0.7 (1–2)
<i>Cy. caeruleus</i>	0 (0/27)	-	0 (0/13)	-
<i>D. syriacus</i>	0 (1)	-	16.7 (1/6)	1
<i>E. rubecula</i>	11.2 (72/644)	2.5 $\pm$ 8.1 (1–68)	10.7 (63/590)	1.9 $\pm$ 1.4 (1–7)
<i>Fi. albicollis</i>	0 (0/3)	-	4.2 (1/24)	1
<i>Fi. hypoleuca</i>	No birds	-	4.6 (2/44)	1.0 $\pm$ 0.0 (1–1)
<i>Fi. parva</i>	0 (0/215)	-	0 (0/16)	-
<i>Fr. coelebs</i>	0 (0/10)	-	0 (0/46)	-
<i>I. pallida</i>	0 (0/7)	-	2.9 (5/172)	1.0 $\pm$ 0.0 (1–1)
<i>J. torquilla</i>	No birds	-	7.7 (1/13)	1
<i>Lo. luscinioides</i>	No birds	-	12.5 (1/8)	1
<i>Lu. luscinia</i>	4.7 (3/64)	1.7 $\pm$ 1.2 (1–3)	0 (0/24)	-
<i>Lu. megarhynchos</i>	0 (0/10)	-	13.3 (6/45)	1.2 $\pm$ 0.4 (1–2)
<i>M. striata</i>	0 (0/51)	-	0 (0/16)	-
<i>O. scops</i>	0 (0/3)	-	12.5 (2/16)	1.0 $\pm$ 0.0 (1–1)
<i>Pa. major</i>	3.2 (1/31)	1.0	0 (0/33)	-
<i>Pho. phoenicurus</i>	7.7 (7/91)	1.3 $\pm$ 0.5 (1–2)	11.1 (1/9)	1
<i>Phy. collybita</i>	0 (0/152)	-	(11/293)	1.6 $\pm$ 0.8 (1–3)
<i>Phy. trochilus</i>	0.7 (1/149)	1	0 (0/22)	-
<i>Pr. modularis</i>	0 (0/23)	-	16.7 (7/42)	1.4 $\pm$ 0.5 (1–2)
<i>S. atricapilla</i>	0.5 (3/669)	1	1.5 (10/649)	1.1 $\pm$ 0.3 (1–2)
<i>Tr. troglodytes</i>	0 (0/3)	-	21.4 (3/14)	1.0 $\pm$ 0.0 (1–1)
<i>Tu. iliacus</i>	0 (0/1)	-	33.3 (1/3)	7
<i>Tu. merula</i>	31.3 (20/64)	2.8 $\pm$ 4.0 (1–15)	46.3 (44/95)	3.4 $\pm$ 5.9 (1–39)
<i>Tu. philomelos</i>	7.1 (3/42)	1.3 $\pm$ 0.6 (1–2)	13.8 (11/80)	1.5 $\pm$ 0.7 (1–3)
<i>Tu. viscivorus</i>	No birds	-	No birds	-
Total	3.9 (110/2830)	2.3 $\pm$ 6.8 (1–68)	6.6 (191/2879)	2.1 $\pm$ 3.1 (1–39)
Bird species	Autumn 2021		Spring 2022	
	Prevalence	Mean intensity (range)	Prevalence	Mean intensity $\pm$ SD (range)
<i>Ac. palustris</i>	0 (0/5)	-	0 (0/19)	-
<i>Ac. schoenobaenus</i>	0 (0/5)	-	0 (0/6)	-
<i>Ac. scirpaceus</i>	33.3 (1/3)	1	0 (0/17)	-
<i>An. trivialis</i>	0 (0/6)	-	4.8 (1/21)	1
<i>Ca. europaeus</i>	0 (0/9)	-	25.0 (1/4)	1
<i>Ce. cetti</i>	0 (0/57)	-	16.7 (5/30)	3.0 $\pm$ 3.9 (1–10)
<i>Cu. communis</i>	0 (0/25)	-	0 (0/25)	-
<i>Cu. curruca</i>	2.3 (1/44)	5	0 (0/48)	-
<i>Cu. melanocephala</i>	0 (0/37)	-	5.9 (1/17)	1
<i>Cy. caeruleus</i>	6.7 (3/45)	1.7 $\pm$ 0.6 (1–2)	0 (0/6)	-
<i>D. syriacus</i>	No birds	-	0 (0/3)	-

**Table 1** (continued)

<i>E. rubecula</i>	21.0 (203/966)	6.1±10.0 (1–64)	7.4 (11/149)	2.7±2.8 (1–10)
<i>Fi. albicollis</i>	No birds	-	0 (0/85)	-
<i>Fi. hypoleuca</i>	No birds	-	(1/166)	1
<i>Fi. parva</i>	5.3 (13/244)	1.9±1.5 (1–6)	0 (0/11)	-
<i>Fr. coelebs</i>	14.3 (3/21)	2.0±1.0 (1–3)	(0/1)	-
<i>I. pallida</i>	No birds	-	2.7 (4/146)	2.3±1.0 (1–3)
<i>J. torquilla</i>	0 (0/1)	-	0 (0/2)	-
<i>Lo. luscinioides</i>	No birds	-	0 (0/1)	-
<i>Lu. luscinia</i>	No birds	-	10.0 (1/10)	1
<i>Lu. megarhynchos</i>	0 (0/4)	-	0 (0/43)	-
<i>M. striata</i>	0 (0/17)	-	2.3 (2/44)	1
<i>O. scops</i>	0 (0/4)	-	14.3 (1/7)	8
<i>Pa. major</i>	1.7 (1/58)	2	5.3 (1/19)	1
<i>Pho. phoenicurus</i>	5.8 (5/86)	1.8±1.8 (1–5)	(1/4)	1
<i>Phy. collybita</i>	4.4 (8/183)	2.8±3.1 (1–10)	(4/164)	1.3±0.5 (1–2)
<i>Phy. trochilus</i>	2.0 (3/151)	2.0±1.0 (1–3)	0 (0/5)	-
<i>Pr. modularis</i>	10.0 (4/40)	2.3±2.5 (1–6)	19.1 (4/21)	1.5±1.0 (1–3)
<i>S. atricapilla</i>	0.9 (6/655)	2.7±2.9 (1–8)	0.7 (3/464)	1.0±0.0 (1–1)
<i>Tr. troglodytes</i>	8.7 (2/23)	3.5±2.1 (2–5)	13.4 (2/13)	1.5±0.5 (1–2)
<i>Tu. iliacus</i>	0 (0/3)	-	No birds	-
<i>Tu. merula</i>	33.7 (28/83)	10.4±27.5 (1–142)	64.0 (34/63)	5.2±5.3 (1–22)
<i>Tu. philomelos</i>	8.1 (8/99)	2.4±2.5 (1–8)	16.7 (3/18)	2.3±2.3 (1–5)
<i>Tu. viscivorus</i>	10.0 (1/10)	1	No birds	-
Total	9.4 (290/3096)	5.7±11.8 (1–142)	4.3 (80/1846)	3.4±4.1 (1–22)

**Table 2** Comparison of the seasonality of tick infestation mean intensity for each bird species and each tick infestation mean intensity for all birds. (Asymptotic significances are displayed. The significance level is .05)

Compared records	Null hypothesis	Test	Comparison of tick infestation mean intensity for each bird species seasonally		Comparison of each tick infestation mean intensity for all birds seasonally	
			Sig.	Decision	Sig.	Decision
All seasons (2020 Autumn, 2021 Spring, 2021 Autumn, and 2022 Spring)	The distribution of intensity is the same across categories of the seasons	Independent samples Kruskal-Wallis test	.028	Reject the null hypothesis	.680	Retain the null hypothesis
2020 and 2021 Autumn		Independent samples	.045*		.843*	
2021 Spring and 2021 Autumn		Mann-Whitney <i>U</i> test	.003*		.319*	
2021 Autumn and 2022 Spring			.039*		.590*	
1st and 2nd ringing year			.101	Retain the null hypothesis	.917	
2020 Autumn and 2021 Spring			.881*		.319*	
2020 Autumn and 2022 Spring			.892*		.514*	
2021 and 2022 Spring			.792		.887*	

\*Exact significance is displayed for this test

A total of 2573 ticks were found on 671 of the 10,651 birds examined. The numerical distribution of developmental stages of ticks was 1946 (75.6%) larvae, 554 (21.5%) nymphs, and 73 (2.8%) adults, respectively. The larvae and nymphs of *Hyalomma* species were described at the genus level because morphological species identification is unreliable for the immatures. In contrast, some larvae of *Ixodes* species could not be identified at the species level due to morphological deformation occurring during the collection and preservation process. As a result, the ticks and their numbers (ratio in total ticks) were as follows: 70 (2.7%) *Ixodes* spp. larvae, 1829 (71.1%) *Ixodes frontalis* larvae, 39 (1.5%) *Ixodes ricinus* larvae, 7 (0.3%) *Hyalomma* spp. larvae, 1 (0.04%) *Haemaphysalis* sp. larva, 337 (13.1%) *I. frontalis* nymphs, 16 (0.6%) *Ixodes acuminatus* nymphs, 141 (5.5%) *I. ricinus* nymphs, 60 (2.3%) *Hyalomma* spp. nymphs, 30 (1.2%) *I. frontalis* adults, 1 (0.04%) *I. ricinus* adult, and 42 (1.6%) *I. acuminatus* adults. All but one (*I. acuminatus* collected from *E. rubecula* in March 2021) of the collected 73 adults were females. The highest number of larvae, nymphs, and adults seen on a single individual were 140 (*Tu. merula* in October 2021), 32 (*Tu. merula* in April 2021), and 3 (*Tu. merula* in March 2021), respectively (Supplementary file 2, Table 3).

The analysis to determine the seasonal characteristics of tick infestation showed the prevalence of *Ixodes* spp. larvae is higher in the autumn (5.6) than in the spring (1.7) periods. However, the prevalence was higher in all tick species or genera in the spring, except for *Haemaphysalis* sp. larva, of which only one sample was found (on *E. rubecula* in October 2021). This difference was remarkably higher in *I. frontalis* nymphs, *Hyalomma* spp. nymphs, and *I. acuminatus* adults. The prevalence of these three ticks was 2.3, 0.7, and 0.7 in the spring period and 1.2, 0.2, and 0.1 in the autumn period, respectively. A similar difference was also found in the infested bird's seasonal characteristics of tick intensity. In *Ixodes* spp. larvae, the mean intensity was  $5.5 \pm 0.66$  (range: 1–140) in the autumn and  $2.6 \pm 0.27$  (range: 1–14) in the spring, respectively. In all other ticks (except *Haemaphysalis* sp. larva), the mean intensity increased by more than 10% in spring compared to autumn, e.g., this increase was 76.9% in *I. frontalis* nymphs, 36.4% in *Hyalomma* spp. nymphs, and 10% in *I. acuminatus* adults (Table 4, Figs. 2 and 3).

The records showed that 86.3% of birds were infested with only one of the ten identified tick groups. The probability of birds being infested with two, three, four, and five different tick groups was calculated as 10.6%, 2.5%, 0.5%, and 0.2%, respectively. Among the tick groups, the co-existence probability of *I. acuminatus* nymph, *I. frontalis* nymph, *I. ricinus* nymph, *Hyalomma* spp. nymph, *I. frontalis* adult, *I. acuminatus* adult, and *Ixodes* spp. larva with at least one other tick group was 57.2%, 45.3%, 34.1%, 11.4%, 44%, 33.3%, and 16.4%, respectively.

In the evaluations to determine whether there is any relationship between the migratory categories of birds and

characteristics of tick infestation, the L migrants and R and RS migrants examined in the spring periods (2021 and 2022 together) were used. (other migration categories and periods were not considered since the boundaries between migration territories and category characters are not decisively defined.) It was found that the prevalence of *Ixodes* spp. larvae, *I. frontalis* nymphs, *I. acuminatus* nymphs, *I. ricinus* nymphs, *I. frontalis* adults, and *I. acuminatus* adults were higher on the R and RS migrants (21.1, 71.6, 6.4, 20.2, 9.2, and 15.6%, respectively) than the L migrants (13.3, 4.4, 2.2, 17.8, 2.2, and 6.7%, respectively). Similarly, the average intensities ( $\pm$ SE) of the same species were higher on the R and RS migrants ( $3.2 \pm 0.70$ ,  $2.6 \pm 0.29$ ,  $1.3 \pm 0.18$ ,  $2.7 \pm 1.28$ ,  $1.5 \pm 0.27$ , and  $1.1 \pm 0.08$ , respectively) compared to the L migrants ( $2.8 \pm 1.1$ , 1.0, 1.0,  $1.1 \pm 0.13$ , 1.0, 1.0, and 1.0, respectively). However, a completely different result was obtained in *Hyalomma* spp. nymphs. Although the prevalence and mean intensity in the L migrants were 60.0 and  $1.6 \pm 0.25$ , respectively, no specimen of this tick was encountered in R and RS migrants. The species of birds (migration category and number of infested birds) with *Hyalomma* spp. nymphs in the spring periods are: *I. pallida* (L, 9 birds), *Ac. palustris* (L, 4 birds), *O. scops* (L, 3 birds), *Pho. phoenicurus* (L, 2 birds), *Lu. megarhynchos* (L, 2 birds), *Fi. hypoleuca* (L, 2 birds), *Ac. schoenobaenus* (L, 2 birds), *Cu. communis* (L, 1 bird), *Ca. europaeus* (L, 1 bird), *An. trivialis* (L, 1 bird), *S. atricapilla* (SML, 4 birds), and *E. rubecula* (RSM, 1 bird).

Of the 47 *Hyalomma* nymphs collected in the spring periods of 2021 and 2022, 17 were fully engorged. These ticks were collected from 11 birds belonging to the following six species: *O. scops* (1 nymph in March 2021 and 5 nymphs from a bird in April 2022), *I. pallida* (1 nymph in May 2021, 1 nymph in June 2021, 2 nymphs from a bird in May 2022, and 1 nymph in June 2022), *Pho. phoenicurus* (1 nymph in April 2022), *S. atricapilla* (1 nymph in April 2021 and 1 nymph in May 2022), *Ac. schoenobaenus* (1 nymph in May 2021), and *Ac. palustris* (1 nymph in June 2021) (Fig. 3). The nymphs were taken into the tubes and incubated with total exposure to the local climatic conditions of Eastern Thrace. In July, the molting and activation (the pre-feeding process of the adults) of all the nymphs were completed in both years. All the adults were morphologically identified as *Hyalomma rufipes*, 15 females and two males (one male was collected from *Ac. palustris* in June 2021 and the other from *I. pallida* in May 2022).

## Discussion

In this study, ticks' prevalence and average intensity were 6.3% and  $3.8 \pm 0.33$  (range: 1–142) in 10,651 birds examined. These values are within the range of other studies conducted on wild birds in the Western Palearctic. Reports from

Table 3 Numbers and species of ticks encountered on birds

Period	Bird	Number infested/ examined in total	Tick number			Adult					
			Larva	Nymph	Adult	<i>I. ricinus</i>	<i>I. frontalis</i>	<i>I. acuminatus</i>			
Autumn period 2020	Species		<i>Ixodes Hyalomma</i>	<i>I. frontalis</i>	<i>I. ricinus</i>	<i>Hyalomma</i>	<i>I. frontalis</i>	<i>I. ricinus</i>	<i>I. acuminatus</i>		
	<i>E. rubecula</i>	72/644	167	1	-	2	1	6	-	1	
	<i>Lu. luscinia</i>	3/64	4	-	-	-	1	-	-	-	
	<i>Pa. major</i>	1/31	-	-	-	-	-	1	-	-	
	<i>Pho. phoenicurus</i>	7/91	7	-	-	-	-	2	-	-	
	<i>Phy. trochilus</i>	1/149	-	-	-	-	1	-	-	-	
	<i>S. atricapilla</i>	3/669	1	-	-	-	1	-	1	-	
	<i>Tu. merula</i>	20/64	47	-	-	3	4	1	-	1	
	<i>Tu. philomelos</i>	3/42	1	-	-	2	1	-	-	-	
	Periodic total	110/2830	227	1	-	7	9	10	1	2	
	Spring period 2021	<i>Ac. palustris</i>	4/35	-	-	-	-	1	6	-	-
		<i>Ac. schoenobaenus</i>	2/4	-	-	-	-	-	3	-	-
		<i>An. trivialis</i>	1/13	-	-	-	-	-	1	-	1
<i>Ce. cetti</i>		5/59	6	-	-	2	-	-	-	-	
<i>Cu. communis</i>		6/56	5	1	-	-	5	1	-	-	
<i>Cu. curruca</i>		1/116	2	-	-	-	-	-	-	-	
<i>Cu. melanocephala</i>		2/83	-	-	-	-	-	3	-	-	
<i>D. syriacus</i>		1/6	-	-	-	-	-	-	-	1	
<i>E. rubecula</i>		63/590	76	2	-	26	7	2	-	5*	
<i>Fi. albicollis</i>		1/24	-	-	-	-	1	-	-	-	
<i>Fi. hypoleuca</i>		2/44	-	-	-	-	-	2	-	-	
<i>I. pallida</i>		5/172	-	-	-	-	-	5	-	-	
<i>J. torquilla</i>		1/13	-	-	-	-	-	-	-	1	
<i>Lu. luscinioides</i>	1/8	-	-	-	-	-	-	-	1		
<i>Lu. megarhynchos</i>	6/45	1	-	-	-	1	3	1	-		
<i>O. scops</i>	2/16	-	-	-	1	-	-	-	-		
<i>Pho. phoenicurus</i>	1/9	-	-	-	-	-	1	-	-		
<i>Phy. collybita</i>	11/293	13	-	-	1	3	-	-	-		
<i>Pr. modularis</i>	7/42	-	-	-	2	2	1	-	5		

Table 3 (continued)

Period	Bird	Periodic total	Number infested/ examined in total	Tick number			Nymph			Adult			
				Larva	Nymph	Adult	Larva	Nymph	Adult	Larva	Nymph	Adult	
Autumn period 2021	<i>S. atricapilla</i>	10/649		-	2	-	-	6	2	-	-	1	
	<i>Tr. troglodytes</i>	3/14		1	-	-	1	-	-	-	-	1	
	<i>Tu. iliacus</i>	1/3		7	-	-	-	-	-	-	-	-	
	<i>Tu. merula</i>	44/95		19	1	-	80	40	3	-	-	7	
	<i>Tu. philomelos</i>	11/80		-	-	-	11	2	-	-	-	3	
	Periodic total	191/2879		130	6	-	124	1	26	6	1	26	
	Species			Number infested/ examined in total	Larva	Nymph <td>Adult</td> <td><i>Ixodes</i></td> <td><i>Haemaphysalis</i></td> <td><i>I. ricinus</i></td> <td><i>I. frontalis</i></td> <td><i>I. ricinus</i></td> <td><i>I. acuminatus</i></td>	Adult	<i>Ixodes</i>	<i>Haemaphysalis</i>	<i>I. ricinus</i>	<i>I. frontalis</i>	<i>I. ricinus</i>	<i>I. acuminatus</i>
	<i>Ac. scirpaceus</i>	1/3		1	-	-	-	-	-	-	-	-	-
	<i>Cu. curruca</i>	1/44		5	-	-	-	-	-	-	-	-	-
	<i>Cy. caeruleus</i>	3/45		5	-	-	-	-	-	-	-	-	-
	<i>E. rubecula</i>	203/966		1153	1	50	15	1	2	-	-	1	
	<i>Fi. parva</i>	13/244		24	-	1	-	-	-	-	-	-	
	<i>Fr. coelebs</i>	3/21		6	-	-	-	-	-	-	-	-	
<i>Pa. major</i>	1/58		-	-	2	-	-	-	-	-	-		
<i>Pho. phoenicurus</i>	5/86		7	-	1	-	-	1	-	-	-		
<i>Phy. collybita</i>	8/183		22	-	-	-	-	-	-	-	-		
<i>Phy. trochilus</i>	3/151		6	-	-	-	-	-	-	-	-		
<i>Pr. modularis</i>	4/40		-	-	-	-	-	7	-	1	-		
<i>S. atricapilla</i>	6/655		16	-	-	-	-	-	-	-	-		
<i>Tr. troglodytes</i>	2/23		7	-	-	-	-	-	-	-	-		
<i>Tu. merula</i>	28/83		240	-	30	13	2	4	-	-	2		
<i>Tu. philomelos</i>	8/99		15	-	3	1	-	-	-	-	-		
<i>Tu. viscivorus</i>	1/10		-	-	-	-	-	1	-	-	-		
Periodic total	290/3096		1507	1	87	36	3	9	4	-	4		
Spring period 2022	<i>An. trivialis</i>	1/21		-	-	1	-	-	-	-	-	-	
	<i>Ca. europaeus</i>	1/4		-	-	-	-	1	-	-	-	-	
	<i>Ce. cetti</i>	5/30		9	-	1	4	1	-	-	-	-	
	<i>Cu. melanocephala</i>	1/17		-	-	-	-	-	1	-	-	-	

Table 3 (continued)

<i>E. rubecula</i>	11/149	-	-	5	-	2	1	-	-	1
<i>Fi. hypoleuca</i>	1/166	-	-	-	-	-	-	1	-	-
<i>I. pallida</i>	4/146	-	-	-	-	-	9	-	-	-
<i>Lu. luscinia</i>	1/10	-	-	-	-	1	-	-	-	-
<i>M. striata</i>	2/44	-	-	-	-	-	-	-	-	-
<i>O. scops</i>	1/7	-	-	1	-	-	7	-	-	-
<i>Pa. major</i>	1/19	-	-	-	-	-	-	1	-	-
<i>Pho. phoenicurus</i>	1/4	-	-	-	-	-	1	-	-	-
<i>Phy. collybita</i>	4/164	-	-	2	-	-	-	-	-	-
<i>Pr. modularis</i>	4/21	-	-	-	-	3	-	-	-	2
<i>S. atricapilla</i>	3/464	-	-	-	-	-	1	2	-	-
<i>Tr. troglodytes</i>	2/13	-	-	-	-	-	-	-	-	-
<i>Tu. merula</i>	34/63	-	-	104	8	16	-	11	-	6
<i>Tu. philomelos</i>	3/18	-	-	3	-	-	-	-	-	1
Periodic total	80/1846	-	-	119	9	25	21	14	-	10
Total	671/10651	1938	7	337	16	141	60	30	1	42

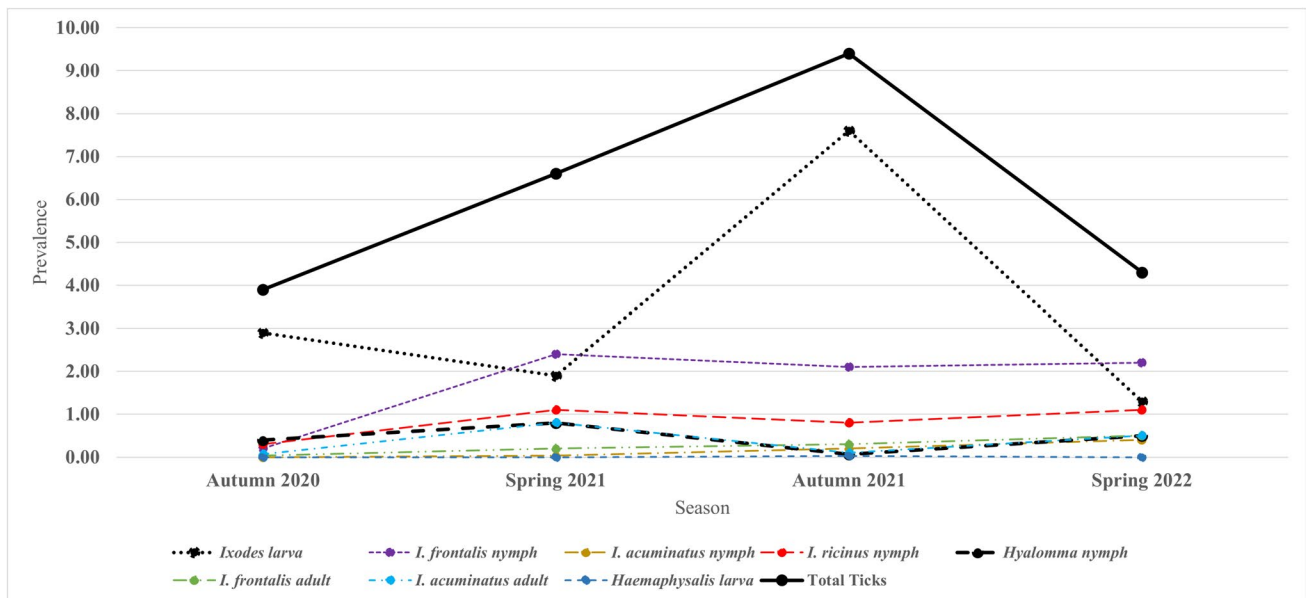
\*One male, four females

**Table 4** Prevalence and mean intensity of ticks in birds examined in different periods

Ticks	Autumn 2020			Spring 2021		
	<i>n</i>	Prevalence	Intensity $\pm$ SD (range)	<i>n</i>	Prevalence	Intensity $\pm$ SD (range)
<b>Larvae</b>						
<i>Ixodes</i>	227	2.9 (83/2830)	2.7 $\pm$ 7.8 (1–68)	130	1.9 (55/2879)	2.4 $\pm$ 1.6 (1–7)
<i>Hyalomma</i>	1	0.04 (1/2830)	1	6	0.2 (5/2879)	1.2 $\pm$ 0.5 (1–2)
<i>Haemaphysalis</i>	-	-	-	-	-	-
<b>Nymphs</b>						
<i>I. frontalis</i>	7	0.2 (6/2830)	1.2 $\pm$ 0.4 (1–2)	124	2.4 (68/2879)	1.8 $\pm$ 1.5 (1–7)
<i>I. acuminatus</i>	-	-	-	1	0.04 (1/2879)	1
<i>I. ricinus</i>	9	0.3 (8/2830)	1.1 $\pm$ 0.4 (1–2)	71	1.1 (32/2879)	2.2 $\pm$ 5.0 (1–29)
<i>Hyalomma</i>	10	0.4 (10/2830)	1.0 $\pm$ 0.0 (1–1)	26	0.8 (22/2879)	1.2 $\pm$ 0.5 (1–3)
<b>Adults</b>						
<i>I. frontalis</i>	1	0.04 (1/2830)		6	0.2 (6/2879)	1.0 $\pm$ 0.0 (1–1)
<i>I. ricinus</i>	-	-	-	1	0.04 (1/2879)	1
<i>I. acuminatus</i>	2	0.07 (2/2830)	1.0 $\pm$ 0.0 (1–1)	26	0.8 (24/2879)	1.1 $\pm$ 0.3 (1–2)
<b>Total</b>	257	3.9 (110/2830)	2.3 $\pm$ 6.8 (1–68)	391	6.6 (191/2879)	2.0 $\pm$ 3.1 (1–39)
<b>Autumn 2021</b>						
<b>Larvae</b>						
<i>Ixodes</i>	1507	7.6 (235/3096)	6.4 $\pm$ 12.8 (1–140)	74	1.3 (23/1846)	3.2 $\pm$ 3.6 (1–14)
<i>Hyalomma</i>	-	-	-	-	-	-
<i>Haemaphysalis</i>	1	0.03 (1/3096)	1	-	-	-
<b>Nymphs</b>						
<i>I. frontalis</i>	87	2.1 (64/3096)	1.4 $\pm$ 1.0 (1–7)	119	2.2 (40/1846)	3.0 $\pm$ 3.3 (1–17)
<i>I. acuminatus</i>	6	0.2 (6/3096)	1.0 $\pm$ 0.0 (1–1)	9	0.4 (7/1846)	1.3 $\pm$ 0.5 (1–2)
<i>I. ricinus</i>	36	0.8 (24/3096)	1.5 $\pm$ 1.1 (1–6)	25	1.1 (21/1846)	1.2 $\pm$ 0.5 (1–3)
<i>Hyalomma</i>	3	0.07 (2/3096)	1.5 $\pm$ 0.7 (1–2)	21	0.5 (10/1846)	2.1 $\pm$ 1.9 (1–7)
<b>Adults</b>						
<i>I. frontalis</i>	9	0.3 (9/3096)	1.0 $\pm$ 0.0 (1–1)	14	0.5 (9/1846)	1.6 $\pm$ 0.9 (1–3)
<i>I. ricinus</i>	-	-	-	-	-	-
<i>I. acuminatus</i>	4	0.1 (4/3096)	1.0 $\pm$ 0.0 (1–1)	10	0.5 (9/1846)	1.1 $\pm$ 0.3 (1–2)
<b>Total</b>	1653	9.4 (290/3096)	5.7 $\pm$ 11.8 (1–142)	272	0.6 (80/1846)	3.4 $\pm$ 4.1 (1–22)
<b>Spring 2022</b>						

the studies can often be quite different from one another. The prevalence ranged from 0.5 to 5% in some research (e.g., Keskin and Erciyas-Yavuz 2016; Hoffman et al. 2021; Zajac et al. 2022), while values between 6 and 40.5% have been reported in some others (e.g., Hoogstraal et al. 1961; Nowak-Chmura et al. 2012; Ciebiera et al. 2019; Klitgaard et al. 2019; Wilhelmsson et al. 2020; Rollins et al. 2021). It is well known that birds' characteristics of tick infestation are driven by many intrinsic and environmental parameters (Buczek et al. 2020; Sormunen et al. 2022; Wimbauer et al. 2022). Consistent with this fact, the current study revealed that the prevalence and intensity could vary dramatically depending on several factors, such as (i) the bird species and, therefore, its feeding habits, habitat preference, migration routes, and categories, and stopover sites used on the way of migration; (ii) tick species and thus their seasonal activation pattern, geographical distribution characteristics, and host specificity; and (iii) the month, season, and locality of the study (Tables 1, 3, and 4,

Supplementary file 2). However, it also does not seem easy to predict the severity of the individual effects of each of these interacting drivers. Although this study was conducted in the same region, various degrees of incompatibility were observed between the prevalence, intensity, and species distribution in the same season for two consecutive years, even in the same bird species (Tables 1, 3, and 4). It is possible to associate this discrepancy with changes in the phenology or population density of ticks, which may be caused by the periodical characteristics of climatic and environmental factors (Kar and Gargili Keles 2021) prevailing in the breeding grounds, wintering grounds, or on the migration routes of the birds. In addition, climatic and environmental changes can also affect the overall phenology of bird migration (Ambrosini et al. 2016; Usui et al. 2017). Any differentiation in the timing of migration and tick activation, on the other hand, can ultimately lead to temporary isolation between birds and ticks, which can directly affect the infestation characteristics.



**Fig. 2** Seasonal distribution characteristics of tick numbers in wild birds captured in Turkish Thrace



**Fig. 3** Photos of some ticks feeding on birds: *Ixodes* spp. larva on *Tu. merula* (A), female *I. ricinus* on *Tu. philomelos* (B), *Ixodes* sp. nymph on *E. rubecula* (C), *I. frontalis* nymph (D) and *H. rufipes* nymph (E) on *O. scops*, and *H. rufipes* nymph on *Ca. europaeus* (F)

This study showed that the tick species carried by the same bird species could change significantly in the spring and autumn period (Table 4). This result is not a surprise since the geographical distribution pattern of ticks (Estrada-Peña et al. 2017; Horak et al. 2018) and the birds' breeding grounds, wintering areas, and autumn and spring migration routes are different (Fig. 1). For instance, unlike the distribution patterns of most other tick species in the Western Palearctic, *I. ricinus* with high bird affinity is relatively prevalent and has exceptionally high population densities in the northern territories of Europe and the Black Sea basin (Estrada-Peña et al. 2017). This fact directly affected the study's total prevalence and intensity, favoring the autumn period. Similar compatibility was recorded in *I. frontalis* and *I. acuminatus* (Table 4). Although these two species have a relatively wide-range distribution in the Western Palearctic, they are known to be more common in the Mediterranean Basin and central Europe (Estrada-Peña et al. 2017). Consistently, the species were found with higher prevalence and intensity in the birds coming from the south in the spring periods compared to the autumn, and this result agrees with the records reported from the birds in Southern Europe (Hoogstraal et al. 1963; Diakou et al. 2016; Buczek et al. 2020; Toma et al. 2021; Hornok et al. 2022).

Seven larvae and 60 nymphs belonging to the genus *Hyalomma* were found on the birds. Of those, six larvae and 47 nymphs were encountered in the spring and the others in the autumn (Table 4). Seventeen engorged nymphs sampled from the birds of the six bird species examined in the spring periods were incubated with total exposure to the local climatic conditions of Thrace. They completed the molting process in July and were morphologically identified as *H. rufipes* adults. All these six bird species have long-distance migration characteristics. This transport is expected considering the geographical distribution of *H. rufipes*, i.e., sub-Saharan Africa and, to a lesser extent, the Nile Delta and the Red Sea basin (Apanaskevich and Horak 2008). Due to the variable temperature and humidity conditions, which the ticks are exposed to during migration (Schmaljohann et al. 2007; Buczek et al. 2020), the immature stages (larva and nymph) of two-host tick *H. rufipes* can remain on the host for up to 4 weeks or more before the detachment as engorged nymphs (Hoogstraal 1956; Hoogstraal et al. 1961). This prolonged feeding period and high bird affinity can allow this species to reach the northern parts of the Western Palearctic via migrating birds (Grandi et al. 2020; Hubálek et al. 2020). The studies carried out in Cyprus (Kaiser et al. 1974) and Aegypt (Hoogstraal et al. 1961, 1963, 1964), which are used by the birds passing through Thrace, have revealed that the percentage of *Hyalomma* immatures in total ticks can reach up to 95%, the prevalence in total birds can be more than 10%, the intensity may exceed ten in some birds, and the rate of the larvae in the immatures may be around 30% in some cases. In the territories to north of Thrace, the prevalence, intensity, and rate

of larvae dramatically decrease on the way to spring migration (Nuorteva and Hoogstraal 1963).

In this study, no significant difference was revealed in terms of tick infestation prevalence between birds that spend their feeding time mainly on the ground and mostly in non-ground environments such as trees and bushes. However, when birds were considered individually, it was observed that some specific feeding behaviors may be crucial in the infestation of some bird species such as *Erithacus rubecula*, *Turdus merula*, *Fringilla coelebs*, and *Passer domesticus*. All four bird species spend most of their time on the ground. The first two species tend to rummage under leaves and other debris in wooded areas and search for food such as worms. They are likely exposed to high tick infestation due to this behavior. The last two species feed on ready-made seeds and fruits on the ground and tend to move relatively quickly and forage. This behavior makes it particularly logical that there are few ticks on these two birds. The fact that sparrow, the last bird species, spends most of their time in grassy areas close to people where ticks are likely to be less common, seems to be a factor that reduces the density of ticks in this species.

This study indicates that a large number of engorged nymphs of *H. rufipes* can reach Anatolia and Thrace every year in the spring, molt to adults under the circumstances of local climatic conditions, and have the opportunity to feed on animals. Although rarely, the adults of the species can be found on hosts such as cows, horses, and humans in Anatolia, Thrace, and other parts of Europe in summer and autumn (e.g., Bakirci et al. 2011; Chitimia-Dobler et al. 2016; Hansford et al. 2019; Grandi et al. 2020; Kar and Gargili Keles 2021; Uiterwijk et al. 2021). However, no permanent population of *H. rufipes* has yet been accurately shown in Europe. In a recent study, a possible establishment was suspected in central Europe based on the evaluations of 11 nymphs and one larva collected from 505 birds captured during the spring migration (May and June) (Keve et al. 2023). This assertion needs field-based proof for some reasons. For instance, the immatures of *H. rufipes* have been routinely found on different bird species during this season for a long time in Europe (e.g., Hoogstraal et al. 1961, 1964; Kaiser et al. 1974; Grandi et al. 2020; Rollins et al. 2021; Toma et al. 2021); however, while the larvae and nymphs of *H. marginatum*, a similar tick species indigenous to Western Palearctic, can be frequently reported in birds in autumn period (e.g., Hoogstraal et al. 1963, 1964), the immatures of *H. rufipes* were not found in autumn, neither in this study nor the others performed in Europe. Furthermore, the presence of larvae in birds in the spring raises the question at what stage and how the tick survived the winter under the climatic circumstances of central Europe.

The establishment failure of *H. rufipes* in Europe has been associated with climatic parameters, such as low temperature and high humidity, particularly in central and northern Europe (Hoogstraal et al. 1961; Grandi et al. 2020;

Hoffman et al. 2021). The habitat and climatic preferences, hosts, and biology of the sub-Saharan tick *H. rufipes* and the Western Palearctic tick *H. marginatum* are comparable. The primary hosts for the larvae and nymphs of these two-host ticks are leporids, insectivores, and various ground-dwelling birds, while cattle and some other large ungulates, wild or domestic, are the preferred hosts for the adults. *Hyalomma rufipes* is distributed mainly in the arid and semiarid parts of Africa, which differ from each other to a certain extent in terms of temperature regimes and ecological characteristics (Hoogstraal et al. 1961; Apanaskevich and Horak 2008). Although *H. marginatum* is also known as an arid environment species, its adaptation competence to different temperature and humidity levels and some other geographical and ecological drivers is high, and because of this ecological plasticity, it is widely distributed in the Western Palearctic (Hoogstraal 1956; Apanaskevich and Horak 2008; Kar and Gargili Keles 2021). Our current research and many other studies carried out in the Western Palearctic (e.g., Hoogstraal et al. 1961; Hoogstraal et al. 1963; Hoffman et al. 2021; Toma et al. 2021) indicate that a significant number of engorged nymphs of these two tick species can cross the Sahara by birds to the south (i.e., *H. marginatum*) or north (i.e., *H. rufipes*). Furthermore, it is known that some ecologically and climatically similar areas in Sub-Saharan Africa and the Western Palearctic fall within the range of *H. rufipes* and *H. marginatum* habitat characteristics to varying degrees (Hoogstraal et al. 1961). The fact that these two species could not be established widely in both Africa and Europe (Estrada-Peña et al. 2017; Horak et al. 2018), despite all these facilitating conditions, indicates that some complicated and patterned biological, ecological, and/or climatic factors seem to be forcing *H. rufipes* and *H. marginatum* into a kind of wide-range scale segregation, the boundary of which is the Sahara or its extensions.

In a recent field-based study on horses in southern France, new colonization of *H. marginatum* was precisely shown. The researchers underlined that year-long warm temperatures, low precipitation, moderate annual humidity, a predominance of open natural habitats, such as sclerophyllous vegetated and sparsely vegetated areas, and reachable host are the crucial factors for the establishment (Bah et al. 2022). Interestingly, although these factors are also preferred for *H. rufipes* in its native territories (Hoogstraal 1956; Hoogstraal et al. 1961), and although this species can enter the area through the migrating birds (Rollins et al. 2021; Toma et al. 2021), at least as much as *H. marginatum*, *H. rufipes* could not be colonized in the area. Likewise, although some *H. marginatum*-prevalent areas in Anatolia and Thrace also seem to be favorable for *H. rufipes* in some respects, such as climate, vegetation, and host availability, no establishment of this species was proven in Turkey (Kar and Gargili Keles 2021; Kar et al. 2021). All this indicates that some factors

may prevent the permanent establishment of *H. rufipes* in Europe and some other regions of the Western Palearctic.

In history, it can be assumed that the migration pattern of wild birds belonging to different migration routes and associated tick and agent flows has followed mostly a similar feature for long periods due to relatively stable environmental conditions (Charmantier and Gienapp 2014; Dutta 2017; Bókony et al. 2019). It is possible that this regular pattern has contributed to the formation of endemic stability (Kar and Gargili Keles 2021; Kar and Ergunay 2021) within the range of migratory birds, and any change in this regularity can affect the stability negatively. For example, it is predicted that the ongoing climate change will affect the time spent in the stopover sites and the wintering and breeding areas (Charmantier and Gienapp 2014; Bókony et al. 2019). There is also the possibility that climate change will make some sites suitable for the establishment of new ticks and/or agents (Kar and Gargili Keles 2021; Kar and Ergunay 2021; McCoy et al. 2023). Human-caused environmental destruction in the wintering, breeding, and resting areas can cause some alterations in the characteristics of migration routes and ranges (Møller et al. 2014; Ambrosini et al. 2016; Usui et al. 2017; Bókony et al. 2019). All these conditions will confirm the transport and possible invasion risk of new ticks and agents to new areas. Furthermore, the rapidly increasing human population, the progressive aggregation of the human population, particularly on the seaside, and the tendency of birds to use suitable areas closest to the shore for refueling and resting, particularly after the overseas flight (Hahn et al. 2009; Dutta 2017; Hoffman et al. 2021) increase the risk of bird-human contact. As is probably the case for many regions around the world, although urbanization is relatively high on the coastline in Thrace due to afforestation, the proportion of wooded areas (fruit trees, evergreens, tropical culture plants, etc.) is mostly higher compared to the inner parts of Thrace, which are primarily composed of agricultural lands. These wooded urban areas can be used to feed and shelter by birds. All these trends can force the wild birds, and therefore their ticks and agents, to urbanize and potentially increase the risk of relevant human diseases. Consistent with this correlation, most human cases of WNV infection in Thrace, the annual incidence of which is known to be directly related to the annual climate and bird migration patterns (Kilpatrick 2011), are mainly observed on the shores of the Sea of Marmara (the reports of the Ministry of Health of the Republic of Turkey; <https://www.saglik.gov.tr/>).

## Conclusions

This study shows that (i) Thrace, which is the most critical bottleneck on the Mediterranean/Black Sea Flyway, is in a privileged position at the point of transportation of the tropical ticks

from the Afrotropical realm to Europe, (ii) due to its climatic and ecological characteristics and geographical location, the region seems to be ideal for monitoring the bird migration and related risks and making future predictions, (iii) although the bird migration between Africa and Europe has been continuing primarily in a specific order over a long historical period, the associated medical risk from the birds themselves or their ticks is much higher today than in the past, and it is possible to predict that this risk will increase even more in the future, and (iv) it appears that the share of direct human impact on nature in this increase, particularly through habitat destructions, will be at least as much or perhaps much more than the share of the contemporary climate change alone.

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**Author contribution** S.K., E.B., V.B., and A.G.K. conceived the ideas and designed the methodology. E.B., A.C.O., U.G. carried out the bird examination. S.K. and G.A. performed the tick identification. S.K. and D.B. evaluated the results and wrote the manuscript. All authors contributed to editing and gave final approval for publication.

**Data availability** The datasets generated during the current study are available in the Results and Supplementary files repository.

## Declarations

**Ethical approval** Ethical approval does not apply to for this study. The sampling of birds was approved by the General Directorate of Nature Conservation and National Parks, Ministry of Agriculture and Forestry, Republic of Turkey (protocol number 26137614-280.01.01-E.2141100 12.07.2019).

**Consent for publication/consent to participate** Not applicable.

**Competing interests** The authors declare no competing interests.

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