



Review Article

A review on the role of birds as disseminators of ticks, with special emphasis on *Hyalomma* species and Crimean-Congo haemorrhagic fever virus

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ABSTRACT

Hyalomma marginatum and *Hyalomma rufipes* are tick species of high medical importance, primarily due to their ability to transmit the Crimean-Congo haemorrhagic fever virus. While *H. marginatum* is endemic in Southern Europe, *H. rufipes* maintains viable populations exclusively in Africa. Nevertheless, adult specimens of both tick species are frequently detected in non-endemic regions of Europe. This phenomenon is primarily driven by bird migration, during which these two-host ticks can be transported over great distances. To enhance our understanding of the role of birds in the dispersal of *Hyalomma* ticks and their potential contribution to the passive transmission of Crimean-Congo haemorrhagic fever virus, this mini review was compiled. By synthesizing relevant articles, the summary aims to contribute to a more precise understanding of the phenomenon. According to our findings, the relationship between bird-transported *Hyalomma* species and Crimean-Congo haemorrhagic fever is highly complex from an eco-epidemiological perspective. A better understanding of the direct association between migratory birds and the virus, as well as the mechanisms of viral persistence and transmission, is essential for developing effective risk assessment strategies.

1. Introduction

In Europe, 38 tick species have been recorded from birds so far (Keve et al., 2022; Pitó et al., 2024). Among these, *Ixodes ricinus* is the most common species in Central and Northern Europe (Keve et al., 2022). While birds are important hosts and disseminators of ticks in a local aspect and take part in the transmission cycle of several tick-borne (and other arthropod-borne) pathogens of veterinary and public health significance (e.g., *Borrelia garinii* and West Nile virus), one of their greatest eco-epidemiological significances comes from the long distance, even transcontinental migration, of some species. During this, birds are able to introduce various taxa of non-native blood-sucking ectoparasites to Europe (Keve et al., 2023; 2024b). Among these, *Hyalomma* species, mainly *Hyalomma marginatum* and *Hyalomma rufipes*, are inevitably the most important in an eco-epidemiological aspect. This is mainly due to their ability to transmit Crimean-Congo haemorrhagic fever virus (CCHFV) (Hoogstraal, 1979; Turell, 2007), a pathogen with a potential high human mortality, as it can manifest as an asymptomatic to mild

disease or a haemorrhagic fever with a case fatality rate of approximately 30 % (Eslava et al., 2024). In the past, numerous studies have been conducted to investigate the relationship between *Hyalomma* ticks and migratory birds (Capek et al., 2014; Keve et al., 2023; Wallménius et al., 2014)). However, the links between ticks arriving in Europe via bird migration routes and the emergence of CCHFV in new areas remain subject to considerable uncertainty. The aim of this mini-review is to provide an overview of the current data and associations concerning the tick life stages found on birds across various European countries, and to identify existing knowledge gaps that need to be addressed to better understand the potential role of birds in the ecology and transmission of CCHFV.

2. Materials and methods

In order to compile this review, our previous work (Keve et al., 2022) served as a basis. The resulting information was supplemented with the relevant data published since then, accessible in the google scholar

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database, and with those that were omitted from the aforementioned work. In Tables 1 and 2 only those references were used which provided the tick-host associations accurately. Data were omitted if not informative in this context or if the tick/host species were uncertain. In some cases, such as Martyn (1988) and Toma et al. (2021), the studies did not always provide detailed information on all specific bird–tick associations. However, they did report the developmental stages of *Hyalomma* species found on birds across different locations. Similarly, uncertain identifications of *Hyalomma* spp. are represented in both Fig. 1 and Fig. 2 when no other reliable data were available from the respective regions. Species were considered uncertain when *H. marginatum* sensu lato (probably *H. rufipes*) (Lindeborg et al., 2012), appeared, or if *H. rufipes* was identified based solely on morphology at a subadult stage (Saikku et al., 1971). In order to assess the migratory status of the bird species and their overwintering areas the publicly available data of the BirdLife organization was used (BirdLife International, 2025). To assess the migratory status of a specific bird species in a specific country, not only the written data, but also the maps provided by BirdLife were considered.

English bird species names are capitalized, following international recommendations by Gill and Donsker (2012) (<http://www.worldbirdnames.org/>). The taxonomic classification of birds is presented in accordance with BirdLife International (2025).

2.1. Review of literature data on birds as disseminators of *Hyalomma* species

2.1.1. *Hyalomma marginatum*

Hyalomma marginatum is a two-host tick (meaning the larva and the nymph are both feeding on the same host individual, on which nymphal moulting occurs), spending approximately 12–26 days on its first host, which opens the possibility of long distance transportation by migratory birds (Estrada-Peña et al., 2011). Due to the fact that *H. marginatum* is endemic in Southern Europe (Estrada-Peña et al., 2017), it is not surprising that this tick (chiefly larvae and nymphs) is commonly found on resident (sedentary) birds in Southern Europe, but also on short distance migrants in Central Europe. The larvae on migratory birds were found in Central and Northern Europe (Table 1, Fig. 1). In Central Europe, freshly moulted nymphs on migratory birds are also common finds (own, unpublished observations). Although adults have been reported to feed on birds, some of these observations are uncertain, as moulting may have occurred after sample collection (Capek et al., 2014). In contrast to *H. rufipes*, *H. marginatum* predominates on birds (both resident and migratory) in the Iberian Peninsula and South-Eastern Europe. Interestingly, in Italy, *H. marginatum* is heavily outnumbered by *H. rufipes* on spring-migrant birds (approximately to a 1:5 ratio (Mancuso et al., 2022), or ~1:4 (Toma et al., 2021) despite the fact that *H. marginatum* is endemic in that country. Similar observations were made in Malta, where *H. rufipes* greatly outnumbered *H. marginatum* on birds (Hornok et al., 2022). This is despite the fact that, according to the statistical model by Burnus et al. (2025), *H. marginatum* is more likely to parasitize birds than *H. rufipes*. However, the latter study is built on pan-European results. The potential spreading of *H. marginatum* was modelled based on data between 2002 and 2018 (Estrada-Peña et al., 2021). Despite the high importance of the latter study, several new records from various locations in Europe had been recorded in the past seven years (e.g., Hornok et al., 2022; Keve et al., 2024a; Mancuso et al., 2022; Sándor et al., 2021; Wilhelmsson et al., 2020) (Table 1).

2.1.2. *Hyalomma rufipes*

The presence of *H. rufipes* on birds during the spring migration period is not uncommon in warmer countries. *Hyalomma rufipes* is a two-host tick, spending on average 22.8 days on the first host individual (Estrada-Peña et al., 2017), but generally between 21 and 29 days (Magano et al., 2000). According to the available data, this tick, as a larva or nymph, can be transported to Northern-European countries,

such as Norway and Finland, but is considerably more common on migratory birds in Southern European countries like Malta, Italy, and Southern France (Keve et al., 2022). Almost all the avian hosts of *H. rufipes* recorded in Europe fall into the long-distance migrant category, except for the European Robin (*Erithacus rubecula*), Song Thrush (*Turdus philomelos*) (resident/ short-distance migrants in Europe), and Bearded Reedling (*P. biarmicus*) (resident) (Table 2). In 1964, nymphs of *H. rufipes* were collected in Finland (Saikku et al., 1971). The report was published in 1971, well before the invention of PCR and the rise of molecular identification methods. Nowadays, morphology alone is considered to be inadequate for the differentiation of the immature stages of *H. rufipes* from *H. marginatum* (Estrada-Peña et al., 2017), therefore, while not being necessarily erroneous, this report has to be interpreted with caution. The authors themselves acknowledge the uncertainty surrounding some of these findings (Saikku et al., 1971). The northernmost finding of *H. rufipes* larva in Europe so far was recorded in Hungary (Keve et al., 2023). Within Central Europe, all *H. rufipes* specimens found on migratory birds until now were already in the nymphal stage (Hornok et al., 2016; Hubálek et al., 2020; Keve et al., 2024a, 2023, 2022). Interestingly, the larva was collected from a resident, non-migrant bird (Bearded Reedling). Adult *H. rufipes* ticks are exceedingly rare on birds. In contrast, there have been reports of several males and females of this species feeding on Sedge Warbler (*Acrocephalus schoenobaenus*) and Barn Swallow (*Hirundo rustica*) found in Corsica, as documented in Matsumoto et al. (2004). The cited article does not specify whether these ticks were indeed feeding on the birds. Given that these are the only known instances of adult *H. rufipes* being associated with migrating birds (to the best of our knowledge), these findings are unlikely to significantly alter the general understanding that adults of this species typically do not feed on passerine birds. Adults can be found on ostriches, although they are considered “less preferred” hosts of *H. rufipes* (Estrada-Peña et al., 2017). In earlier research done in Egypt between 1956 and 1960, 1025 ticks were collected from birds migrating to Europe and Asia, 1018 of which were *H. rufipes* (Hoogstraal et al., 1961). Years later, similar trends were observed in Malta: 78 out of 94 ticks were *H. rufipes* (additional eight specimens had not been identified and were either *H. marginatum* or *H. rufipes*) (Hornok et al., 2022). In a study, conducted on Ventotene Island of Italy, 366/443 of the ticks found on birds were *H. rufipes*. Other Italian studies also reported the predominance of *H. rufipes* on birds (Toma et al., 2014, 2021).

Despite this trend, *H. rufipes* is relatively rare compared to *H. marginatum* on birds caught in continental Europe (Figs. 1 and 2). In the Mediterranean Region, *H. rufipes* is most commonly found on birds that are migrating from sub-Saharan Africa in the direction of Malta, Italy (Hornok et al., 2022; Toma et al., 2014, 2021), and uncommon on birds that are travelling in the direction of Gibraltar. Recently, *H. rufipes* has also been reported from a bird species with a geolocator-tracked origin in Asia (Arabian Peninsula) (Sándor et al., 2025), confirming its arrival in Europe from the eastern direction.

The overwintering areas of the migratory bird species enlisted in Table 2 show a high degree of overlap with the contiguous distribution range of *H. rufipes* in Africa (present in the sub-Saharan region), as well with the sites where smaller populations were observed along the northern coastline of the continent (Burnus et al., 2025; Hoffman et al., 2021; Mancuso et al., 2022; Wallménus et al., 2014). This may explain the Italian findings of *H. rufipes* on resident/short distance migrant birds (European Robin and Song Thrush) (Table 2), as North European populations of these birds may enter northern Africa to overwinter. Based on data from Cyprus, Italy, Malta, and Corsica (Hornok et al., 2022; Kaiser et al., 1974; Mancuso et al., 2022; Matsumoto et al., 2004; Pascucci et al., 2019) the establishment of this species in Mediterranean islands and/or continental Southern Europe cannot be ruled out in the future, as suggested by Hoffman et al. (2021) and Zhou et al. (2025). In this scenario, the exposure of the most common European short/middle distance migrant bird species, e.g.: the European Robin (*E. rubecula*) or the Blackbird (*Turdus merula*), to *H. rufipes* would significantly increase, the

Table 1

The avian hosts of *H. marginatum*, and their migratory status.

Bird Species	Migration status of the host in the country <i>H. marginatum</i> was detected (BirdLife International, 2025)	Overwintering area of European populations (BirdLife International, 2025)	Known life stages found on European birds	Citation (number of reports)
Barn Owl – <i>Tyto alba</i>	Portugal: resident	-	Larva (Portugal), Nymph (Portugal)	(Santos-Silva et al., 2006)
Barn Swallow – <i>Hirundo rustica</i>	Portugal: resident/migrant	Sub-Saharan Africa.	Nymph (Portugal)	(Santos-Silva et al., 2006)
Black Kite – <i>Milvus migrans</i>	Portugal: migrant	Predominantly in sub-Saharan Africa.	Nymph (Portugal)	(Santos-Silva et al., 2006)
Bluethroat – <i>Luscinia svecica</i>	Switzerland: migrant Czech Republic: migrant	Mainly migratory, wintering in the Mediterranean Basin and northern Afrotropics.	Nymph (Switzerland, Czech Republic)	(Hubálek et al., 2020; Papadopoulos et al., 2002)
Booted Eagle – <i>Hieraaetus pennatus</i>	Portugal: migrant	Sub-Saharan Africa.	Nymph (Portugal)	(Santos-Silva et al., 2011)
Collared Flycatcher – <i>Ficedula albicollis</i>	Sweden: migrant	Sub-Saharan Africa. The migration routes and wintering areas are poorly known.	Larva (Sweden)	(Jaenson et al., 1994)
Common Chaffinch – <i>Fringilla coelebs</i>	Spain: resident Sweden: resident/migrant	Depending on latitude: resident, partially migratory or migratory. Seldom reaches Africa.	Larva (Spain) Female (Sweden)	(Palomar et al., 2015; Wilhelmsson et al., 2020)
Common Kestrel – <i>Falco tinnunculus</i>	Portugal: resident Slovenia: resident Malta: resident (migrating through) Denmark: migrant	Only northern populations are migrant: to sub-Saharan Africa.	Larva (Portugal, Spain) Nymph (Portugal, Malta, Denmark) Unknown (Slovenia)	(Hornok et al., 2022; Hubálek et al., 2020; Jaenson et al., 1994; Santos-Silva et al., 2011)
Common Kingfisher – <i>Alcedo atthis</i>	Portugal: resident Malta: overwintering	Southern populations: sedentary. Northern populations: to Western-Europe, Southern-Europe, North Africa, Middle East. Sub-Saharan Africa, Afrotropics.	Nymph (Portugal, Malta)	(Santos-Silva et al., 2011, 2006)
Common Nightingale – <i>Luscinia megarhynchos</i>	Spain: migrant Czech Republic: migrant Bulgaria: migrant Italy: migrant Slovakia: migrant		Larva (Portugal, Czech Republic) Nymph (Spain, Czech Republic, Bulgaria, Italy, Slovakia) Unknown (Italy)	(Aleksandrova et al., 2021; Capek et al., 2014; Hubálek et al., 2020; Mancuso et al., 2022; Palomar et al., 2015; Toma et al., 2014)
Common Redstart – <i>Phoenicurus phoenicurus</i>	United Kingdom: migrant Switzerland: migrant Italy: migrant Germany: migrant Slovenia: migrant Norway: migrant	Mainly sub-Saharan Africa, but also North Africa, and the southern region of the Arabian Peninsula.	Nymph (United Kingdom, Switzerland, Italy, Germany, Norway) Unknown (Slovenia, Italy, United Kingdom)	(Hubálek et al., 2020; Jameson et al., 2012; Mancuso et al., 2022; Marie-Angèle et al., 2006; Martyn, 1988; Mehl et al., 1984; Papadopoulos et al., 2002; Pascucci et al., 2019)
Common Whitethroat – <i>Curruca communis</i>	United Kingdom: migrant Bulgaria: migrant Germany: migrant Spain: resident/migrant Italy: migrant Malta: no information (likely migrant)	Sub-Saharan Africa.	Nymph (United Kingdom, Bulgaria, Germany, Spain, Malta) Unknown (Italy, United Kingdom)	(Aleksandrova et al., 2021; England et al., 2016; Hornok et al., 2022; Hubálek et al., 2020; Jameson et al., 2012; Mancuso et al., 2022; Martyn, 1988)
Common Wheatear – <i>Oenanthe oenanthe</i>	United Kingdom: migrant	In Africa (Sahel and sub-Saharan Africa).	Nymph (United Kingdom)	(Jameson et al., 2012)
Dunnoek – <i>Prunella modularis</i>	France: resident Italy: resident	North Africa and the Mediterranean. Migratory status depends on geographical location.	Nymph (France) Unknown (Italy)	(Mancuso et al., 2022; Vial et al., 2016)
Domestic Chicken – <i>Gallus gallus domesticus</i>	Romania: resident	-	Unknown (Romania)	(Mihalca et al., 2012)
Eurasian Blackbird – <i>Turdus merula</i>	Portugal: resident Spain: resident Ukraine: resident/migrant Italy: resident (migrating through)	Depending on latitude: southern-Europe, South-west Asia, North-Africa.	Larva (Portugal, Spain) Nymph (Portugal, Spain, Ukraine) Unknown (Italy)	(Akimov and Nebogatkin, 2011; Norte et al., 2013; Palomar et al., 2015; Santos-Silva et al., 2006; Toma et al., 2014)
Eurasian Buzzard – <i>Buteo buteo</i>	Portugal: resident Italy: mostly resident (migrating through)	Mostly resident in Europe, but some migrate to southern Europe or northwest Africa.	Nymph (Portugal) Unknown (Italy)	(Santos-Silva et al., 2011; Toma et al., 2014)
Eastern Olivaceous Warbler – <i>Iduna pallida</i>	Greece: migrant	The northern race migrates to east/northeast Africa and southwest Arabia, while North African breeders winter in the Sahel, Sudan, or Eritrea.	Nymph (Greece)	(Diakou et al., 2016)
Eurasian Blackcap – <i>Sylvia atricapilla</i>	Sweden: migrant/ resident Germany: migrant Italy: resident (migrating through)	Migratory status depends on geographical location. Found in parts of Northern, Western, and Eastern Africa.	Larva (Sweden) Nymph (Germany) Unknown (Italy)	(Hubálek et al., 2020; Jaenson et al., 1994; Toma et al., 2014)
Eurasian Blue Tit – <i>Cyanistes caeruleus</i>	Portugal: resident Spain: resident	-	Nymph (Portugal, Spain)	(Palomar et al., 2015; Santos-Silva et al., 2006)

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Table 1 (continued)

Bird Species	Migration status of the host in the country <i>H. marginatum</i> was detected (BirdLife International, 2025)	Overwintering area of European populations (BirdLife International, 2025)	Known life stages found on European birds	Citation (number of reports)
Eurasian Eagle-owl – <i>Bubo bubo</i>	Portugal: resident Bulgaria: resident	-	Larva (Bulgaria) Nymph (Bulgaria, Portugal) Male (Bulgaria) Unknown (Italy)	(Sándor et al., 2021; Santos-Silva et al., 2011, 2006)
Eurasian Golden Oriole – <i>Oriolus oriolus</i>	Italy: migrant	Equatorial African high woodlands and moist montane forests of East Africa.	Unknown (Italy)	(Mancuso et al., 2022)
Eurasian Hoopoe – <i>Upupa epops</i>	Slovenia: migrant	Northern populations are fully migratory: to the Mediterranean and Africa, including the Sahel and sub-Saharan Africa. Southern populations are partially migratory or sedentary.	Unknown (Slovenia)	(Hubálek et al., 2020)
Eurasian Jay – <i>Garrulus glandarius</i>	Portugal: resident	-	Nymph (Portugal)	(Norte et al., 2013)
Eurasian Reed Warbler – <i>Acrocephalus scirpaceus</i>	Slovakia: migrant Czech Republic: migrant Portugal: migrant Switzerland migrant Germany: migrant Norway: migrant	Sub-Saharan Africa.	Larva (Slovakia) Nymph (Portugal, Norway) Female (Switzerland, Czech Republic) Male (Switzerland) Unknown (Germany)	(Capek et al., 2014; Mehl et al., 1984; Papadopoulos et al., 2002; Petney et al., 2012; Santos-Silva et al., 2011, 2006)
Eurasian Stonechat – <i>Saxicola torquatus</i>	Portugal: resident	Migratory status depends on geographical location. Overwinters in southern-Europe, North Africa and in the Arabian Peninsula. Sub-Saharan Africa.	Nymph (Portugal)	(Santos-Silva et al., 2011, 2006)
Eurasian Scops Owl – <i>Otus scops</i>	Italy: resident/migrant	Sub-Saharan Africa.	Unknown (Italy)	(Mancuso et al., 2022)
Eurasian Tree Sparrow – <i>Passer montanus</i>	Portugal: resident	Mostly sedentary. Birds in the extreme north may migrate to the south.	Nymph (Portugal)	(Santos-Silva et al., 2006)
European Greenfinch – <i>Chloris chloris</i>	Spain: resident Portugal: resident	Some populations of the species are migratory while others are sedentary. They can overwinter in North Africa.	Nymph (Portugal, Spain)	(Palomar et al., 2015; Santos-Silva et al., 2006)
European Goldfinch – <i>Carduelis carduelis</i>	Italy: resident	Migratory status depends on geographical location. Some can travel to North Africa and to the Middle East.	Unknown (Italy)	(Mancuso et al., 2022)
European Nightjar – <i>Caprimulgus europaeus</i>	Italy: migrant	Mainly in south and east Africa, with small numbers in West Africa.	Nymph (Italy)	(Pascucci et al., 2019)
European Pied Flycatcher – <i>Ficedula hypoleuca</i>	Spain: migrant	West Africa.	Larva (Spain)	(Palomar et al., 2015)
European Robin – <i>Erithacus rubecula</i>	Sweden: resident/migrant Hungary: resident/migrant Switzerland: resident/migrant Slovakia: resident/migrant France: mostly resident Italy: resident (migrating through)	Migration is poorly understood, and depends on geographical locations. Some of them can overwinter in the Mediterranean and along the northern coast of Africa.	Larva (Sweden, Hungary) Nymph (Switzerland, Hungary, Slovakia, France) Unknown (Italy)	(Hornok et al., 2013; Hubálek et al., 2020; Keve et al., 2024a; Mancuso et al., 2022; Marie-Angèle et al., 2006; Vial et al., 2016; Wilhelmsson et al., 2020)
Eurasian Jackdaw – <i>Corvus monedula</i>	Romania: resident	Sedentary or short-distance migrant in western and southern Europe. Northern birds stay or move southwest, central ones disperse north, and northernmost migrate to the Caspian.	Nymph (Romania)	(Sándor et al., 2017)
Great Reed Warbler – <i>Acrocephalus arundinaceus</i>	Czech Republic: migrant	Sub-Saharan Africa.	Nymph (Czech Republic)	(Capek et al., 2014)
Great Tit – <i>Parus major</i>	Spain: resident Portugal: resident	-	Larva (Spain) Nymph (Spain, Portugal)	(Palomar et al., 2015; Santos-Silva et al., 2006)
House Sparrow – <i>Passer domesticus</i>	Spain: resident	Resident with some short distance migrant populations.	Larva (Spain) Nymph (Spain)	(Palomar et al., 2015)
Iberian Gray Shrike – <i>Lanius meridionalis</i>	Portugal: resident	-	Nymph (Portugal)	(Santos-Silva et al., 2006)
Icterine Warbler – <i>Hyppolais icterina</i>	Italy: migrant	Africa, south of the Equator.	Unknown (Italy)	(Mancuso et al., 2022)
Lesser Kestrel – <i>Falco naumanni</i>	Portugal: resident/migrant	Sub-Saharan Africa, from the Sahel to southern Africa.	Nymph (Portugal)	(Santos-Silva et al., 2011)
Little Owl – <i>Athene noctua</i>	Portugal: resident Romania: resident	Sedentary although large displacements do occur.	Nymph (Portugal) Unknown: Romania	(Mihalca et al., 2012; Santos-Silva et al., 2006)

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Table 1 (continued)

Bird Species	Migration status of the host in the country <i>H. marginatum</i> was detected (BirdLife International, 2025)	Overwintering area of European populations (BirdLife International, 2025)	Known life stages found on European birds	Citation (number of reports)
Marsh Warbler – <i>Acrocephalus palustris</i>	Bulgaria: migrant Slovakia: migrant Czech Republic: migrant Germany: migrant	South-east Africa.	Larva (Slovakia) Nymph (Bulgaria, Slovakia, Germany) Unknown (Czech Republic)	(Aleksandrova et al., 2021; Capek et al., 2014; Hubálek et al., 2020)
Mistle Thrush – <i>Turdus viscivorus</i>	Switzerland: resident Ukraine: resident/migrant	Migratory status depends on geographical location. They can overwinter on North Africa.	Nymph (Switzerland, Ukraine)	(Akimov and Nebogatkin, 2011; Papadopoulos et al., 2002)
Northern Goshawk – <i>Accipiter gentilis</i>	Portugal: resident	Mostly resident, but partially migratory in the northernmost populations. Overwinters mostly in Europe and in the Caucasus.	Nymph (Portugal)	(Santos-Silva et al., 2011)
Ortolan Bunting – <i>Emberiza hortulana</i>	Finland: migrant	Northern part of sub-Saharan Africa.	Nymph (Finland)	(Hubálek et al., 2020)
Red-backed Shrike – <i>Lanius collurio</i>	Norway: migrant	Eastern and southern Africa.	Nymph (Norway)	(Mehl et al., 1984)
Red Kite – <i>Milvus milvus</i>	Portugal: resident	Populations winter within the western breeding range. Small numbers in Morocco.	Larva (Portugal)	(Santos-Silva et al., 2006)
Rook – <i>Corvus frugilegus</i>	Ukraine: resident (migrating through)	Resident over western and southern parts of its range and migratory in the north and east.	Nymph (Ukraine)	(Akimov and Nebogatkin, 2011)
Savi's Warbler – <i>Locustella luscinioides</i>	Slovakia: migrant	Sub-Saharan Africa.	Nymph (Slovakia)	(Capek et al., 2014)
Sedge Warbler – <i>Acrocephalus schoenobaenus</i>	Sweden: migrant United Kingdom: migrant Slovakia: migrant Spain: migrant Poland: migrant Malta: no information (likely migrant)	Sub-Saharan Africa.	Nymph (Sweden, United Kingdom, Slovakia, Spain, Malta) Female (Slovakia) Unknown (Poland, United Kingdom)	(Capek et al., 2014; England et al., 2016; Hornok et al., 2022; Jaenson et al., 1994; Jameson et al., 2012; Martyn, 1988; Nowak-Chmura and Siuda, 2012)
Song Thrush – <i>Turdus philomelos</i>	Hungary: migrant Romania: resident/migrant Italy: resident	Mainly migratory, with southern and western populations being sedentary or partial migrants. Some migrate to Southern Europe, the Mediterranean, and North Africa.	Nymph (Hungary, Romania) Unknown (Italy)	(Keve et al., 2024a; Kolodziejek et al., 2014; Mancuso et al., 2022)
Spotted Flycatcher – <i>Muscicapa striata</i>	Romania: migrant Italy: migrant	Sub-Saharan Africa.	Nymph (Romania) Unknown (Italy)	(Mancuso et al., 2022; Mihalca et al., 2012)
Tawny Owl - <i>Strix aluco</i>	Portugal: resident	-	Nymph (Portugal)	(Santos-Silva et al., 2011)
Tree Pipit – <i>Anthus trivialis</i>	Sweden: migrant Finland: migrant	Afrotropics.	Nymph (Sweden)	(Brinck et al., 1965)
Western Olivaceous Warbler – <i>Iduna opaca</i>	Spain: migrant	West Africa.	Nymph (Spain)	(England et al., 2016)
Western Yellow Wagtail – <i>Motacilla flava</i>	Italy: migrant Poland: migrant	Sub-Saharan Africa.	Nymph (Italy) Unknown (Poland)	(Nowak-Chmura and Siuda, 2012; Pascucci et al., 2019)
Whinchat – <i>Saxicola rubetra</i>	Switzerland: Migrant United Kingdom: migrant	Tropical Africa.	Larva (Switzerland) Nymph (Switzerland) Unknown (United Kingdom)	(Martyn, 1988; Papadopoulos et al., 2002)
White Wagtail – <i>Motacilla alba</i>	Switzerland: resident/migrant Sweden: resident/migrant	Migratory status depends on latitude. They overwinter mainly in Africa, the Mediterranean region and the Middle East.	Nymph (Switzerland, Sweden)	(Jaenson et al., 1994; Papadopoulos et al., 2002)
Willow Warbler – <i>Phylloscopus trochilus</i>	Spain: migrant Malta: no information (likely migrant) Sweden: migrant Norway: migrant	Sub-Saharan Africa but north of the equator and in small numbers in southern Arabia.	Larva (Spain) Nymph (Malta, Sweden, Norway)	(England et al., 2016; Hornok et al., 2022; Mehl et al., 1984; Wilhelmsson et al., 2020)
Wood Warbler – <i>Phylloscopus sibilatrix</i>	Italy: migrant	Sub-Saharan Africa.	Unknown (Italy)	(Mancuso et al., 2022)
Yellowhammer – <i>Emberiza citrinella</i>	Romania: resident	Mainly sedentary, migrating only from the northernmost range in winter, mainly staying in Europe.	Unknown (Romania)	(Mihalca et al., 2012)

potential ratio of ticks reaching even more northern areas of continental Europe (both birds are suitable hosts of subadult stages (Keve et al., 2022)). Therefore, the surveillance of these stop-over sites for possible populations of *H. rufipes* is of high importance.

Local, isolated populations of *H. rufipes* are already established along the Mediterranean coasts of Africa, and are suspected to form

populations in Europe in the future (Hoffman et al., 2021). It was also suspected that *H. rufipes* imported by birds were able to form small, local populations in Russia (Hoogstraal, 1956; Pomerantsev, 1959). The possible overwintering of this species was also suspected in Central Europe (Rudolf et al., 2021). In Hungary, evidence had been found suggestive of the local reproduction of *H. rufipes* (Keve et al., 2023).

Table 2
The avian hosts of *H. rufipes* and their migratory status.

Bird Species	Overwintering area in Africa (BirdLife International, 2025)	Known life stages found in Europe	Citation (number of reports)
Barn Swallow – <i>Hirundo rustica</i>	Sub-Saharan Africa.	Nymph (Malta) Male (Corsica) Unknown (Italy)	(Hornok et al., 2022; Mancuso et al., 2022; Matsumoto et al., 2004)
Black Eared Wheatear - <i>Oenanthe hispanica</i>	African Sahel.	Unknown (Italy)	(Mancuso et al., 2022)
Black Redstart – <i>Phoenicurus ochruros</i>^{*1}	Mostly resident. Northern European populations can migrate to Morocco and Algeria.	Nymph (Italy) Unknown (Italy)	(Battisti et al., 2020; Mancuso et al., 2022; Rollins et al., 2021)
Collared Flycatcher – <i>Ficedula albicollis</i>	Sub-Saharan Africa. The migration routes and wintering areas are poorly known.	Nymph (Malta, Italy) Unknown (Italy)	(Battisti et al., 2020; Hornok et al., 2022; Mancuso et al., 2022; Pascucci et al., 2019; Rollins et al., 2021)
Common Cuckoo – <i>Cuculus canorus</i>	Sub-Saharan Africa. Iberian populations: south of the equator from west Africa to Lake Tanganyika.	Nymph (Italy)	(Pascucci et al., 2019)
Common Nightingale – <i>Luscinia megarhynchos</i>	Sub-Saharan Africa, Afrotropics.	Larva (Italy) Nymph (Italy and France) Unknown (Italy)	(Mancuso et al., 2022; Pascucci et al., 2019; Socolovschi et al., 2012)
Common Redstart – <i>Phoenicurus phoenicurus</i>	Mainly sub-Saharan Africa, but also North Africa, and the southern region of the Arabian Peninsula.	Larva (Italy) Nymph (Italy, Malta and Norway) Unknown (Italy)	(Battisti et al., 2020; Hasle et al., 2009; Hornok et al., 2022; Mancuso et al., 2022; Pascucci et al., 2019; Rollins et al., 2021)
Common Wheatear – <i>Oenanthe oenanthe</i>	Sahel and sub-Saharan Africa (Sahel and sub-Saharan Africa).	Nymph (Italy, Finland, ^{*3} Norway) Unknown (Italy)	(Battisti et al., 2020; Hasle et al., 2009; Mancuso et al., 2022; Pascucci et al., 2019; Rollins et al., 2021; Saikku et al., 1971)
Common Whitethroat – <i>Currucula communis</i>	Sub-Saharan Africa.	Larva (Italy and Malta) Nymph (Italy, Malta, Hungary, Norway) Unknown (Italy)	(Battisti et al., 2020; Hasle et al., 2009; Hornok et al., 2016; Keve et al., 2023; Mancuso et al., 2022; Pascucci et al., 2019; Rollins et al., 2021; Toma et al., 2014)
Eastern Subalpine warbler – <i>Currucula cantillans</i>	Sub-Saharan Africa. Also in North-Western and South-Eastern Algeria and in a small area of Libya.	Larva (Italy) Unknown (Italy)	(Mancuso et al., 2022; Pascucci et al., 2019)

Table 2 (continued)

Bird Species	Overwintering area in Africa (BirdLife International, 2025)	Known life stages found in Europe	Citation (number of reports)
Eastern Woodchat shrike – <i>Lanius senator niloticus</i>	East Africa and rarely in South-Western Arabia.	Nymph (Greece) ^{*3}	(Hoffman et al., 2018)
Eurasian Blackcap – <i>Sylvia atricapilla</i>	Migratory status depends on geographical location. Found in parts of Northern, Western, and Eastern Africa.	Nymph (France)	(Vial et al., 2016)
Eurasian Golden Oriole – <i>Oriolus oriolus</i>	Equatorial African high woodlands and moist montane forests of East Africa.	Nymph (Italy) Unknown (Italy)	(Mancuso et al., 2022; Pascucci et al., 2019; Rollins et al., 2021)
Eurasian Hoopoe – <i>Upupa epops</i>	Northern populations are fully migratory: to the Mediterranean and Africa, including the Sahel and sub-Saharan Africa. Southern populations are partially migratory or sedentary.	Nymph (Malta)	(Hornok et al., 2022)
Eurasian Reed Warbler – <i>Acrocephalus scirpaceus</i>	Sub-Saharan Africa.	Nymph (Italy, Norway, Malta) Unknown (Italy)	(Hasle et al., 2009; Hornok et al., 2022; Mancuso et al., 2022; Pascucci et al., 2019)
Eurasian Wryneck – <i>Jynx torquilla</i>	Western, central and eastern Africa.	Larva (Italy)	(Pascucci et al., 2019)
European Nightjar – <i>Caprimulgus europaeus</i>	Mainly in south and east Africa, with small numbers in West Africa.	Unknown (Italy)	(Mancuso et al., 2022)
European Pied Flycatcher – <i>Ficedula hypoleuca</i>	West Africa.	Larva (Italy, Malta), Nymph (Italy, Malta, Hungary) Unknown (Italy)	(Hornok et al., 2022; Keve et al., 2024, 2023; Mancuso et al., 2022; Pascucci et al., 2019)
European Robin – <i>Erithacus rubecula</i>^{*1}	Migration is poorly understood, and depends on geographical locations. Some of them can overwinter in the Mediterranean and along the northern coast of Africa.	Unknown (Italy)	(Battisti et al., 2020)
European Turtle Dove – <i>Streptopelia turtur</i>	Sub-Saharan Africa.	Larva (Italy)	(Pascucci et al., 2019)
Garden Warbler – <i>Sylvia borin</i>	Sub-Saharan Africa.	Larva (Italy) Nymph (Norway) Unknown (Italy)	(Hasle et al., 2009; Mancuso et al., 2022; Pascucci et al., 2019)

(continued on next page)

Table 2 (continued)

Bird Species	Overwintering area in Africa (BirdLife International, 2025)	Known life stages found in Europe	Citation (number of reports)
Great Reed Warbler – <i>Acrocephalus arundinaceus</i>	Sub-Saharan Africa.	Larva (Italy) Nymph (Italy, Malta)	(Hornok et al., 2022; Pascucci et al., 2019)
Icterine Warbler – <i>Hyppolais icterina</i>	Africa, south of the Equator.	Larva (Italy) Nymph (Italy) Unknown (Italy)	(Mancuso et al., 2022; Pascucci et al., 2019)
Pied Wheatear – <i>Oenanthe pleschanka</i>	Eastern Africa and south-west Arabia.	Nymph (Romania)	(Sándor et al. 2025)
Sedge Warbler – <i>Acrocephalus schoenobaenus</i>	Sub-Saharan Africa.	Nymph (Italy, Malta, Corsica, Greece, Hungary) Male (Corsica) Female (Corsica) Unknown (Italy)	(Hoffman et al., 2018; Hornok et al., 2022; Keve et al., 2023; Mancuso et al., 2022; Matsumoto et al., 2004; Pascucci et al., 2019)
Song Thrush – <i>Turdus philomelos</i>^{*1}	Mainly migratory, with southern and western populations being sedentary or partial migrants. Some migrate to Southern Europe, the Mediterranean, and North Africa.	Unknown (Italy)	(Battisti et al., 2020; Mancuso et al., 2022)
Spotted Flycatcher – <i>Muscicapa striata</i>	Sub-Saharan Africa.	Larva (Italy) Unknown (Italy)	(Battisti et al., 2020; Mancuso et al., 2022; Pascucci et al., 2019)
Thrush Nightingale – <i>Luscinia luscinia</i>	Sub-Saharan Africa.	Nymph (Norway)	(Hasle et al., 2009)
Tree Pipit – <i>Anthus trivialis</i>	Sub-Saharan Africa.	Larva (Italy) Nymph (Italy) Unknown (Italy)	(Mancuso et al., 2022; Pascucci et al., 2019; Rollins et al., 2021)
Western Subalpine Warbler – <i>Curruca iberiae</i>	No data (likely sub-Saharan Africa).	Nymph (Malta)	(Hornok et al., 2022)
Western Yellow Wagtail – <i>Motacilla flava</i>	Sub-Saharan Africa.	Larva (Italy, Greece ^{*3}) Nymph (Finland ^{*3} , Malta) Unknown (Italy)	(Hoffman et al., 2018; Hornok et al., 2022; Mancuso et al., 2022; Saikku et al., 1971)
Whinchat – <i>Saxicola rubetra</i>	Tropical Africa.	Larva (Italy), Nymph (Italy)	(Battisti et al., 2020; Pascucci et al., 2019; Rollins et al., 2021; Toma et al., 2021)
Willow Warbler – <i>Phylloscopus trochilus</i>	Sub-Saharan Africa but north of the equator and in small numbers in southern Arabia.	Larva (Italy, Greece ^{*3}) Nymph (Greece ^{*3}) Unknown (Italy)	(Lindeborg et al., 2012; Mancuso et al., 2022; Pascucci et al., 2019)

Table 2 (continued)

Bird Species	Overwintering area in Africa (BirdLife International, 2025)	Known life stages found in Europe	Citation (number of reports)
Woodchat Shrike – <i>Lanius senator</i>	East Africa and rarely in South-Western Arabia.	Nymph (Malta) Unknown (Italy)	(Hornok et al., 2022; Mancuso et al., 2022)
Wood Warbler – <i>Phylloscopus sibilatrix</i>	Sub-Saharan Africa.	Larva (Italy) Nymph (Malta, Italy) Unknown (Italy)	(Battisti et al., 2020; Hornok et al., 2022; Mancuso et al., 2022; Pascucci et al., 2019)
Bearded Reedling – <i>Panurus biarmicus</i>^{*2}	Resident.	Larva (Hungary) Nymph (Hungary)	(Keve et al., 2023)

^{*1} : The Italian populations are resident/ short distance migrants, but during the spring migration, northern populations that overwintered in North-Africa may travel through Italy.

^{*2} : Resident.

^{*3} : Uncertain tick identification, potentially *H. marginatum*

However, this population was considered unlikely to persist, based on research conducted in the following years in the same area (Keve et al., submitted).

2.2. Other hard ticks of African origin found on European birds

Immatures of other *Hyalomma* species, like *Hyalomma lusitanicum*, *Hyalomma aegyptium*, and *Hyalomma truncatum* are occasionally found on birds in the Mediterranean Basin (Hornok et al., 2022; Keve et al., 2022; Mancuso et al., 2022; Rubel, 2025; Toma et al., 2021), although in relatively small numbers, and are therefore unlikely to bear a high epidemiological importance. In the European part of Turkey, a large number of immature *Hyalomma* ticks (seven larvae and 60 nymphs, species not identified) were found on birds in both spring and fall migration periods between 2020 and 2022 (Bacak et al., 2023). Knowledge on the *Hyalomma* species carried by birds would be crucial in the understanding of the eco-epidemiological role of avian hosts in the transportation of *Hyalomma* species and associated pathogens.

The African ticks *Amblyomma marmoreum* and *Amblyomma variegatum* seem to be regularly recorded on birds that are migrating towards Malta and Italy (Battisti et al., 2020; Hornok et al., 2022; Mancuso et al., 2022; Menegon et al., 2024; Pascucci et al., 2019; Rollins et al., 2021; Toma et al., 2021, 2014), and were also observed on birds in Cyprus (Kaiser et al., 1974). Recently, it was revealed, that some of these ticks may belong to the species *Amblyomma sparsum* (Menegon et al., 2024). In Cyprus, nymphs of *Amblyomma nuttalli* and *Amblyomma lepidum* were also detected (Kaiser et al., 1974).

Adults of *A. variegatum* have been found in Sicily, Corsica, and Sardinia (Toma et al., 2021), as well as in Turkey close to the Syrian border (Aydin and Bakirci, 2007). Adults are seldom found in the southern regions of Continental Europe, like Bulgaria, Greece, and France (Kaiser et al., 1974; Lamontellerie, 1965; Papadopoulos et al., 1996). Based on the above, it can be said that *Amblyomma* species and *H. rufipes* are infesting birds that are following a similar route, although in a much smaller number.

The most common avian host of the European *Amblyomma* ticks seems to be the Tree Pipit (*Anthus trivialis*), with 45 % of all recorded ticks being found on this bird (24/53), based on the following works: Battisti et al., 2020; Hornok et al., 2022; Mancuso et al., 2022; Menegon et al., 2024; Pascucci et al., 2019; Rollins et al., 2021 (we only counted those specimens where the bird hosts were named). The second most

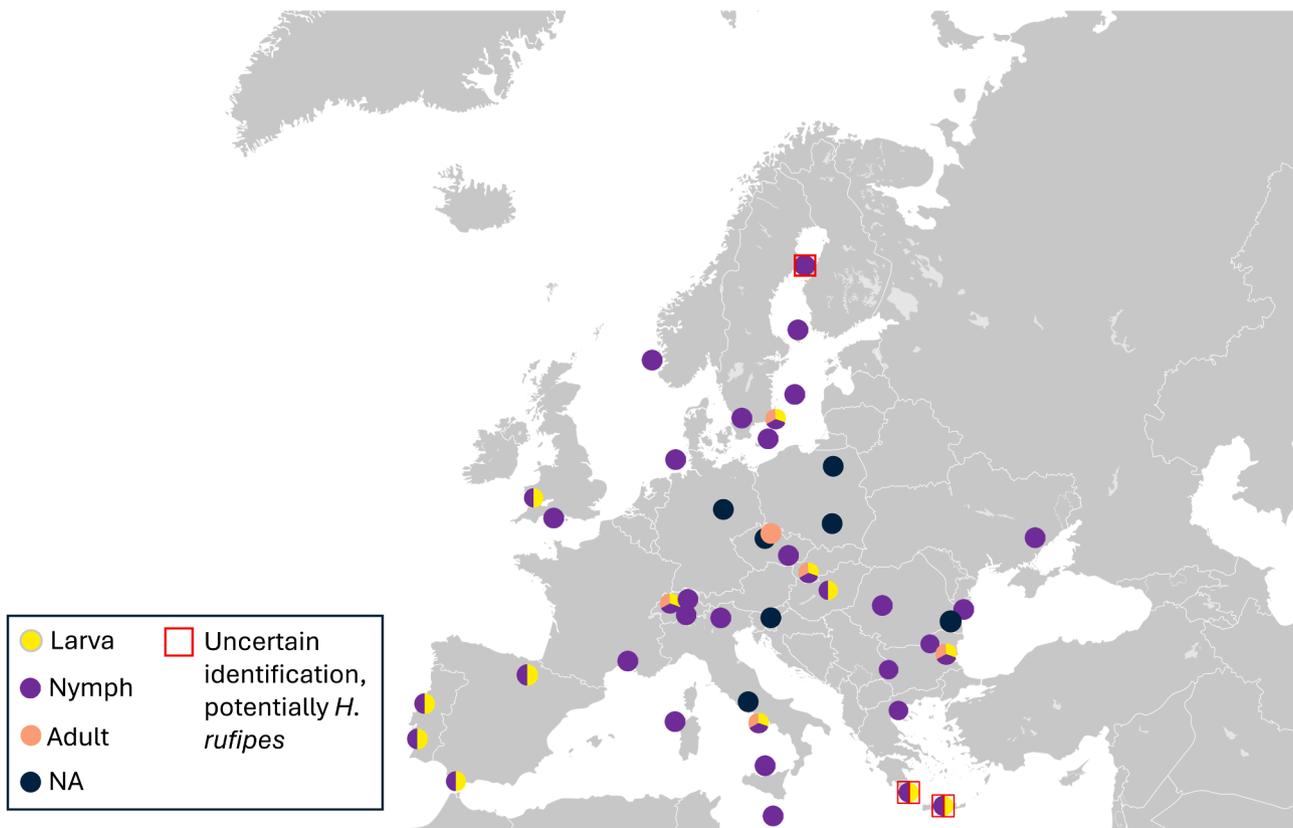


Fig. 1. European distribution of *Hyalomma marginatum* ticks found on birds. Where multiple studies were conducted at the same location, the results are presented in a combined form. Unknown life stages and uncertain identifications are shown only if no more specific data were available from the same site.

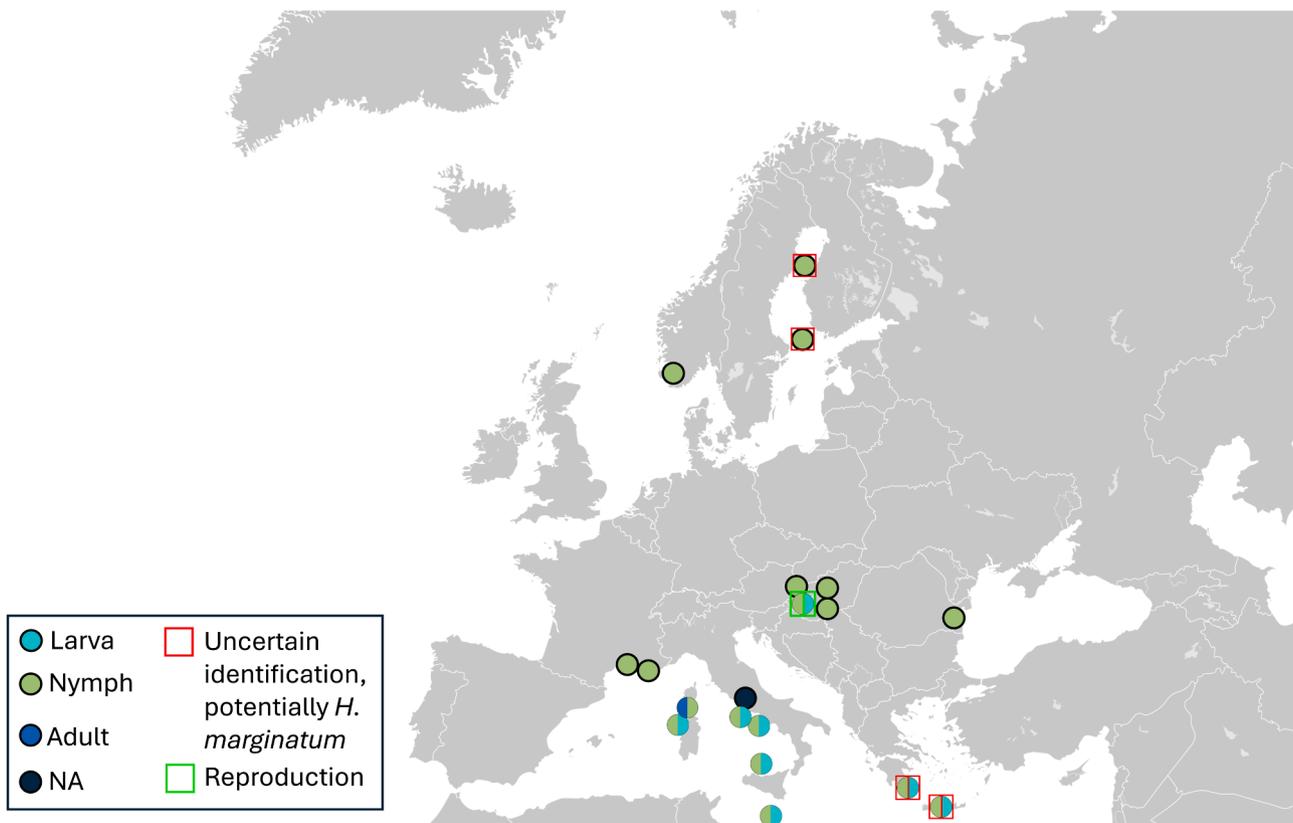


Fig. 2. European distribution of *Hyalomma rufipes* ticks found on birds. Where multiple studies were conducted at the same location, the results are presented in a combined form. Unknown life stages and uncertain identifications are shown only if no more specific data were available from the same site.

common host seems to be the Icterine Warbler (*Hippolais icterina*) with 21 % (11/53) of the recorded ticks.

2.3. The potential eco-epidemiological role of selected birds in the transportation of *Hyalomma* species

The results regarding the Common Wheatear (*Oenanthe oenanthe*) are also worth mentioning. The species shows a Holarctic distribution, with all existing populations (including both Far-Eastern and North American specimens) overwintering in the sub-Saharan region of Africa (BirdLife International, 2025). In addition, it is a regular host of *Hyalomma* nymphs, carrying these as far as northern European countries such as Norway, Finland, and the United Kingdom (Tables 2 and 3). Despite this, it is very unlikely that this bird may introduce *Hyalomma* ticks to America due to the length of the spring migration of American populations which is approximately 55 days. However, it is not unimaginable, based on the fall migration of Canadian populations (29 days) (Bairlein et al., 2012).

The role of the Barn Swallow (*H. rustica*) in *Hyalomma* dissemination is also interesting. This species is a very uncommon host of questing ticks (Keve et al., 2022), due to its unique lifestyle: it is an aerial hawk, feeding exclusively on flying insects (Csörgő et al., 2009), therefore it has little to no connection with questing ticks (Keve et al., 2022). However, both *H. marginatum* and *H. rufipes* have been found on this bird species (one record of *H. marginatum*, and three records of *H. rufipes*) (Tables 1 and 2), likely due to the mentioned ticks' different host-seeking strategies. Barn Swallows breed under the eaves of residential and livestock buildings (Csörgő et al., 2009), so its eco-epidemiological role in relation to *Hyalomma* ticks may deserve attention.

2.4. The potential role of birds in the direct transmission of Crimean-Congo haemorrhagic fever virus

Maybe the most important reason why *H. rufipes* and *H. marginatum* are deserving of attention is their ability to transmit CCHFV (Hoogstraal, 1979; Turell, 2007). However, despite the fact that migratory birds are widely considered the main transcontinental vehicles of the vector ticks, their role in the direct maintenance and transmission of CCHFV is poorly understood (Spengler et al., 2016). Based on what we know so far, most birds seldom develop viraemia, even if infested with CCHFV infected *Hyalomma* ticks. A notable exception is the ostrich (*Struthio camelus*). A low level of viraemia was also observed in the case of Blue helmeted Guinea Fowls (*Numida meleagris*), but most of them appeared to be refractory to the disease (Spengler et al., 2016). In another study, the authors infested different birds (namely Red-billed Hornbills (*Tockus* sp.), Glossy Starlings (*Lamprolornis* sp.), and Domestic Chicken (*Gallus gallus*) with laboratory cultivated, CCHFV naive *H. rufipes* larvae. Even though viraemia was not detectable in any of the birds, antibodies were detected in two bird species (in the hornbill and in the starling). Interestingly, the virus isolation was successful from the nymphs that dropped off from the hornbills, despite the fact that the bird was non-viraemic (Zeller et al., 1994). The transstadial maintenance of CCHFV in *Hyalomma* ticks is poorly understood as well. A previous study showed that although transovarial transmission is highly efficient in the case of *H. rufipes* (more than half of the larvae can become infected transovarially), the infection does not persist past the first generation of ticks. This means, that larvae that are infected through transovarial route, are able to maintain the infection as nymphs, but not as adults (Faye et al., 1999). Unfortunately, research investigating the transstadial maintenance of transovarially infected *H. rufipes* is quite rare. On the other hand, if the tick acquires the virus from the first (avian) host, transstadial maintenance to the adult stage is effective, as pointed out by Zeller et al. (1994). Regarding this phenomenon, Hoogstraal (1979) stated the following: CCHFV is "transmitted transovarially to the F₁ generation (in some cases to F₂) in *Hyalomma m. marginatum*, *H.*

marginatum rufipes, *Dermacentor marginatus*, and *Rhipicephalus rossicus*". In their work, Spengler and Estrada-Peña (2018) also state a similar observation: "When the key hosts for CCHFV circulation are absent, immature *Hyalomma* spp. ticks would use other hosts that are not viraemic, deeply affecting the prevalence of the virus in these vectors."

At the current time, the available data suggest that adult *Hyalomma* ticks moulting from transovarially infected larvae are unlikely to be able to transmit CCHFV if their first host (where they spent larva and nymphal stages) was a migratory bird. In support of this, in a recent study, 175 adult *Hyalomma* ticks (132 *H. marginatum* and 43 *H. rufipes*) collected in Germany between 2019 and 2023 were screened for the presence of Crimean-Congo haemorrhagic fever virus (CCHFV), and all tested negative (Chitimia-Dobler et al., 2024). Similarly, 17 adult *Hyalomma* ticks found in The Netherlands were all PCR-negative for this virus (Uiterwijk et al., 2021).

Although adult *Hyalomma* ticks are routinely found in non-endemic regions of Europe, autochthonous (infection not related to travel) CCHFV cases in these areas are exceedingly rare, if they occur at all (Eslava et al., 2024). This theory would also explain the situation uncovered in Hungary. Here, CCHFV antibodies are commonly detected in animals and humans, but almost always in relatively low titres (Deézi-Magyar et al., 2024; Földes et al., 2019; Magyar et al., 2021; Németh et al., 2013). Although one human CCHFV infection from 2004 was briefly mentioned in a public health report, it does not provide information on the patients' travel history or the diagnostic methods used (Dudás, 2008). Other authors have stated that no human disease has been detected in Hungary so far (Magyar et al., 2021). Although, to the best of our knowledge, CCHFV RNA has never been detected in Hungary, two virus strains antigenically related to the "Congo-antigen group" were isolated from *I. ricinus* nymphs collected in 1972, as determined by cross-neutralization tests (Molnár, 1982).

In Italy, despite the fact that CCHFV was found in nymphs carried by migratory birds, the virus was not found in ground-collected ticks (Mancuso et al., 2022), and we have no knowledge of any human cases (Eslava et al., 2024). Similarly to Hungary, only serological positivity was found in Italy, in transhumant cattle (Fanelli et al., 2022). On the other hand, a serological survey conducted in Italy to detect IgG antibodies against CCHFV in 540 sheep yielded exclusively negative results (De Liberato et al., 2018).

It is important to note, however, that the epidemiology of CCHFV is characterized by the silent persistence of viral foci with sporadic outbreaks (Spengler and Estrada-Peña, 2018). This means that the presence of CCHFV RNA cannot be ruled out in these countries; rather, the virus and vector abundance may simply be too low to result in human cases. However, in both countries, serological prevalence was found in domestic cattle (and sheep in Hungary) (Deézi-Magyar et al., 2024; Fanelli et al., 2022). Since infected animal (or human) blood can occasionally transmit the virus to humans via percutaneous exposure (Izadi et al., 2008), the likelihood of virus-human contact would be elevated in this scenario.

On the other hand, CCHFV infection caused by reattachment of accidentally dislodged *Hyalomma* immatures may be imaginable, as many ticks lose all host-discrimination after the first attachment (Gray et al., 2021). In this context, it is important to mention a *H. marginatum* nymph that was found on a white-breasted hedgehog (*Erinaceus roumanicus*) in the heart of Budapest, Hungary (Földvári et al., 2011), whose presence in the area is difficult to explain. The authors of this article stated that migratory birds might have been the most likely carriers of this specimen (Földvári et al., 2011). It is known that under certain circumstances *H. marginatum* can also behave as a three-host tick (Valcárcel et al., 2020) which would imply rarely larval detachment from the host and moulting to nymph in the environment.

In Spain, the first human CCHFV case was reported in 2013 (Eslava et al., 2024), and in Portugal, the first autochthonous human disease was diagnosed in 2024 (Zé-Zé et al., 2025). Prior to this event, in Portugal CCHFV antibodies were found only in two human patients in 1985

(Filipe et al., 1985). No more cases of CCHF have been detected since then (until 2024), despite the fact that several studies have been conducted on ticks (Zé-Zé et al., 2025). *Hyalomma marginatum* has been endemic in Spain and Portugal, well before these events (Apanaskevich and Horak, 2008).

In conclusion, crucial information is missing to properly assess the role of migrating birds in the direct transmission of CCHFV: 1) The ability of long-distance migrant birds to infect ticks with the virus (and to develop viraemia), 2) The exact mechanism, and persistence, of transstadial maintenance in transovarially infected *Hyalomma* ticks. However, in accordance with other research (Gray et al., 2009; Mancuso et al., 2022), it is highly probable that the establishment of *Hyalomma* populations and the endemisation of CCHFV in a given area follows a different pattern, though likely through connected processes. The presence of *Hyalomma* populations seems to be essential for the virus to become endemic, but their sheer presence does not mean automatic CCHFV occurrence.

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Competing interests

The authors declare no competing interests.

CRedit authorship contribution statement

Gergő Keve: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Data curation, Conceptualization. **Attila D. Sándor:** Writing – review & editing, Validation, Data curation. **Sándor Hornok:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Investigation, Conceptualization.

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No data was used for the research described in the article.

References

Akimov, I.A., Nebogatkin, I.V., 2011. Distribution of the ixodid tick *Hyalomma marginatum* (Acari, Ixodidae) in Ukraine. *Вестник Зоологии* 45, 371–374.

Aleksandrova, N.I., Christova, I., Dimitrov, D., Marinov, M.P., Panayotova, E., Trifonova, I., Taseva, E., Gladnisha, T., Kamenov, G., Ilieva, M., 2021. Records of ixodid ticks on wild birds in Bulgaria. *Probl. Infect. Parasit. Dis.* 49, 35–39.

Apanaskevich, D.A., Horak, I.G., 2008. The genus *Hyalomma* Koch, 1844: v. re-evaluation of the taxonomic rank of taxa comprising the *H. (Euhyalomma) marginatum* koch complex of species (Acari: ixodidae) with redescription of all parasitic stages and notes on biology. *Int. J. Acarol.* 34, 13–42. <https://doi.org/10.1080/01647950808683704>.

Aydin, L., Bakirci, S., 2007. Geographical distribution of ticks in Turkey. *Parasitol. Res.* 101, 163–166. <https://doi.org/10.1007/s00436-007-0694-5>.

Bacak, E., Ozsemir, A.C., Akyildiz, G., Gungor, U., Bente, D., Keles, A.G., Beskardes, V., Kar, S., 2023. Bidirectional tick transport by migratory birds of the African-Western Palearctic flyway over Turkish Thrace: observation of the current situation and future projection. *Parasitol. Res.* 123. <https://doi.org/10.1007/s00436-022-08069-x>.

Bairlein, F., Norris, D.R., Nagel, R., Bulte, M., Voigt, C.C., Fox, J.W., Hussell, D.J.T., Schmaljohann, H., 2012. Cross-hemisphere migration of a 25 g songbird. *Biol. Lett.* 8, 505–507. <https://doi.org/10.1098/rsbl.2011.1223>.

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

BirdLife International, 2025. IUCN Red List for birds [WWW Document]. URL: <https://datazone.birdlife.org>. accessed 2.3.25.

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

Burnus, L., Wynn, J., Liedvogel, M., Rollins, R.E., 2025. Beware of hitchhiking ticks? Clarifying the variable roles of bird species in tick movement along migratory routes. *J. Avian Biol.* 2025, e03275. <https://doi.org/10.1111/jav.03275>.

Capek, M., Literák, I., Kocianova, E., Sychra, O., Najer, T., Trnka, A., Kverek, P., 2014. Ticks of the *Hyalomma marginatum* complex transported by migratory birds into Central Europe. *Ticks Tick-Borne Dis.* 5, 489–493.

Chitimia-Dobler, L., Springer, A., Lang, D., Lindau, A., Facht, K., Dobler, G., Nijhof, A. M., Strube, C., Mackenstedt, U., 2024. Molting incidents of *Hyalomma* spp. Carrying human pathogens in Germany under different weather conditions. *Parasit. Vectors.* 17, 70. <https://doi.org/10.1186/s13071-024-06175-y>.

Csőrgő, T., Karcza, Z., Halmos, G., Magyar, G., Gyurácz, J., Szép, T., Bankovics, A., Schmidt, A., Schmidt, E., 2009. Magyar Madárvonulási Atlasz [Atlas of Bird Migration in Hungary. Kossuth kiadó, Budapest.

De Liberato, C., Frontoso, R., Magliano, A., Montemaggiore, A., Autorino, G.L., Sala, M., Bosworth, A., Scicluna, M.T., 2018. Monitoring for the possible introduction of Crimean-Congo haemorrhagic fever virus in Italy based on tick sampling on migratory birds and serological survey of sheep flocks. *Prev. Vet. Med.* 149, 47–52. <https://doi.org/10.1016/j.prevetmed.2017.10.014>.

Deézi-Magyar, N., Dénes, B., Novák, B., Zsidi, G., Déri, D., Henczkó, J., Pályi, B., Kis, Z., 2024. First broad-range serological survey of Crimean-Congo hemorrhagic fever among Hungarian livestock. *Viruses.* 16, 875. <https://doi.org/10.3390/v16060875>.

Diakou, A., Norte, A.C., Lopes de Carvalho, I., Nuncio, S., Nováková, M., Kautman, M., Alivizatos, H., Kazantzidis, S., Sychra, O., Literák, I., 2016. Ticks and tick-borne pathogens in wild birds in Greece. *Parasitol. Res.* 115, 2011–2016. <https://doi.org/10.1007/s00436-016-4943-3>.

England, M.E., Phipps, P., Medlock, J.M., Atkinson, P.M., Atkinson, B., Hewson, R., Gale, P., 2016. *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. J. Soc. Vector Ecol.* 41, 128–134. <https://doi.org/10.1111/jvec.12204>.

Dudás, M., 2008. Országos Epidemiológiai Központ: krími-Kongó haemorrhagiás láz Görögországban [Crimean-Congo haemorrhagic fever in Greece]. *Épinfo* 27, 313–315.

Eslava, M., Carlos, S., Reina, G., 2024. Crimean-Congo hemorrhagic fever virus: an emerging threat in Europe with a focus on epidemiology in Spain. *Pathogens* 13, 770. <https://doi.org/10.3390/pathogens13090770>.

Estrada-Peña, A., D'Amico, G., Fernández-Ruiz, N., 2021. Modelling the potential spread of *Hyalomma marginatum* ticks in Europe by migratory birds. *Int. J. Parasitol.* 51, 1–11. <https://doi.org/10.1016/j.ijpara.2020.08.004>.

Estrada-Peña, A., Martínez Avilés, M., Muñoz Reoyo, M.J., 2011. A population model to describe the distribution and seasonal dynamics of the tick *Hyalomma marginatum* in the Mediterranean Basin. *Transbound. Emerg. Dis.* 58, 213–223. <https://doi.org/10.1111/j.1865-1682.2010.01198.x>.

Estrada-Peña, A., Mihalca, A.D., Petney, T.N., 2017. Ticks of Europe and North Africa: a Guide to Species Identification. Springer, Cham.

Fanelli, A., Buonavoglia, D., Lanave, G., Monaco, F., Quaranta, V., Catanzariti, R., Ruiz-Fons, F., Buonavoglia, C., 2022. First serological evidence of Crimean-Congo haemorrhagic fever virus in transhumant bovines in Italy. *Transbound. Emerg. Dis.* 69, 4022–4027. <https://doi.org/10.1111/tbed.14710>.

Faye, O., Cornet, J.P., Camicas, J.L., Fontenille, D., Gonzalez, J.P., 1999. Transmission expérimentale du virus de la fièvre hémorragique de Crimée-Congo : place de trois espèces vectrices dans les cycles de maintenance et de transmission au Sénégal. *Parasite* 6, 27–32. <https://doi.org/10.1051/parasite/1999061027>.

Filipe, A.R., Calisher, C.H., Lazuick, J., 1985. Antibodies to Congo-Crimean haemorrhagic fever, Dhori, Thogoto and Bhanja viruses in southern Portugal. *Acta Virol.* 29, 324–328.

Földes, F., Madai, M., Németh, V., Zana, B., Papp, H., Kemenesi, G., Bock-Marquette, I., Horváth, G., Herczeg, R., Jakab, F., 2019. Serologic survey of the Crimean-Congo haemorrhagic fever virus infection among wild rodents in Hungary. *Ticks Tick-Borne Dis.* 10, 101258. <https://doi.org/10.1016/j.ttbdis.2019.07.002>.

Földvári, G., Rigó, K., Jablonszky, M., Biró, N., Majoros, G., Molnár, V., Tóth, M., 2011. Ticks and the city: ectoparasites of the Northern white-breasted hedgehog (*Erinaceus roumanicus*) in an urban park. *Ticks Tick-Borne Dis.* 2, 231–234. <https://doi.org/10.1016/j.ttbdis.2011.09.001>.

Gill, F., Donsker, D., 2012. IOC World Bird Names (version 2.11) [accessed 2025.07.22]. eds. <http://www.worldbirdnames.org/>.

Gray, J., Kahl, O., Zintl, A., 2021. What do we still need to know about *Ixodes ricinus*? *Ticks Tick-Borne Dis.* 12, 101682. <https://doi.org/10.1016/j.ttbdis.2021.101682>.

Gray, J.S., Dautel, H., Estrada-Peña, A., Kahl, O., Lindgren, E., 2009. Effects of climate change on ticks and tick-borne diseases in Europe. *Interdiscip. Perspect. Infect. Dis.* 593232 <https://doi.org/10.1155/2009/593232>, 2009.

- Hasle, G., Bjune, G., Edvardsen, E., Jakobsen, C., Linnehol, B., Røer, J.E., Mehl, R., Røed, K.H., Pedersen, J., Leinaas, H.P., 2009. Transport of ticks by migratory passerine birds to Norway. *J. Parasitol.* 95, 1342–1351. <https://doi.org/10.1645/GE-2146.1>.
- Hoffman, T., Carra, L.G., Öhagen, P., Fransson, T., Barboutis, C., Piacentini, D., Figuerola, J., Kiat, Y., Onrubia, A., Jaenson, T.G.T., Nilsson, K., Lundkvist, Å., Olsen, B., 2021. Association between guilds of birds in the African-western palaearctic region and the tick species *Hyalomma rufipes*, one of the main vectors of Crimean-Congo hemorrhagic fever virus. *One Health* 13, 100349. <https://doi.org/10.1016/j.onehlt.2021.100349>.
- Hoffman, T., Lindeborg, M., Barboutis, C., Erciyas-Yavuz, K., Evander, M., Fransson, T., Figuerola, J., Jaenson, T.G.T., Kiat, Y., Lindgren, P.E., Lundkvist, Å., Mohamed, N., Moutaillier, S., Nyström, F., Olsen, B., Salaneck, E., 2018. Alkhurma hemorrhagic fever virus RNA in *Hyalomma rufipes* ticks infesting migratory birds. *Eur. Asia Minor. Emerg. Infect. Dis.* 24, 879–882. <https://doi.org/10.3201/eid2405.171369>.
- Hoogstraal, H., 1979. The epidemiology of tick-borne Crimean-Congo hemorrhagic fever in Asia, Europe, and Africa. *J. Med. Entomol.* 15, 307–417. <https://doi.org/10.1093/jmedent/15.4.307>.
- Hoogstraal, H., 1956. 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 Nav.* 479–490.
- Hoogstraal, H., Kaiser, M.N., Traylor, M.A., Gaber, S., Guindy, E., 1961. Ticks (Ixodoidea) on birds migrating from Africa to Europe and Asia. *Bull. World Health Organ.* 24, 197–212.
- Hornok, S., Csörgő, T., de la Fuente, J., Gyurancsek, M., Privigyei, C., Meli, M.L., Kreizinger, Z., Gönczi, E., Fernández de Mera, I.G., Hofmann-Lehmann, R., 2013. Synanthropic birds associated with high prevalence of tick-borne rickettsiae and with the first detection of *Rickettsia aeschlimannii* in Hungary. *Vector-Borne Zoonotic Dis.* 13, 77–83.
- Hornok, S., Cutajar, B., Takács, N., Galea, N., Attard, D., Coleiro, C., Galea, R., Keve, G., Sándor, A.D., Kontschán, J., 2022. On the way between Africa and Europe: molecular taxonomy of ticks collected from birds in Malta. *Ticks Tick-Borne Dis.* 13, 102001. <https://doi.org/10.1016/j.ttbdis.2022.102001>.
- Hornok, S., Flaisz, B., Takács, N., Kontschán, J., Csörgő, T., Csipak, Á., Jaksa, B.R., Kovács, D., 2016. Bird ticks in Hungary reflect western, southern, eastern flyway connections and two genetic lineages of *Ixodes frontalis* and *Haemaphysalis concinna*. *Parasit. Vectors.* 9, 101. <https://doi.org/10.1186/s13071-016-1365-0>.
- Hubálek, Z., Sedláček, P., Estrada-Peña, A., Vojtisek, J., Rudolf, I., 2020. First record of *Hyalomma rufipes* in the Czech Republic, with a review of relevant cases in other parts of Europe. *Ticks Tick-Borne Dis.* 11, 101421.
- Izadi, S., Salehi, M., Holakouie-Naieni, K., Chinikar, S., 2008. The risk of transmission of Crimean-Congo hemorrhagic fever virus from human cases to first-degree relatives. *Jpn. J. Infect. Dis.* 61, 494–496. <https://doi.org/10.7883/yoken.JID.2008.494>.
- Jaenson, T.G., Tälleklint, L., Lundqvist, L., Olsen, B., Chirico, J., Mejlom, H., 1994. Geographical distribution, host associations, and vector roles of ticks (Acari: ixodidae, Argasidae) in Sweden. *J. Med. Entomol.* 31, 240–256. <https://doi.org/10.1093/jmedent/31.2.240>.
- Jameson, L.J., Morgan, P.J., Medlock, J.M., Watola, G., Vaux, A.G.C., 2012. Importation of *Hyalomma marginatum*, vector of Crimean-Congo haemorrhagic fever virus, into the United Kingdom by migratory birds. *Ticks Tick-Borne Dis.* 3, 95–99. <https://doi.org/10.1016/j.ttbdis.2011.12.002>.
- Kaiser, M.N., Hoogstraal, H., Watson, G.E., 1974. Ticks (Ixodoidea) on migrating birds in Cyprus, fall 1967 and spring 1968, and epidemiological considerations. *Bull. Entomol. Res.* 64, 97–110.
- Keve, G., Csörgő, T., Benke, A., Huber, A., Mórocz, A., Németh, Á., Kalocs, B., Tamás, E. A., Gyurácz, J., Kiss, O., 2023. Ornithological and molecular evidence of a reproducing *Hyalomma rufipes* population under continental climate in Europe. *Front. Vet. Sci.* 10, 272.
- Keve, G., Csörgő, T., Kovács, D., Hornok, S., 2024a. Long term evaluation of factors influencing the association of ixodid ticks with birds in Central Europe. *Hung. Sci. Rep.* 14, 4958. <https://doi.org/10.1038/s41598-024-55021-9>.
- Keve, G., Sandor, A.D., Hornok, S., 2022. Hard ticks (Acari: ixodidae) associated with birds in Europe: review of literature data. *Front. Vet. Sci.* 9, 928756. <https://doi.org/10.3389/fvets.2022.928756>.
- Keve, G., Csörgő, T., Kovács, D., Benke, A., Bende, A.T., Ágoston, H., Mórocz, J., Németh, Á., Tamás, E.A., Huber, A., Gyurácz, J., Keve, G., Gábor, Kontschán, J., Németh, Á., Hornok, S., 2024b. Contributions to our knowledge on avian louse flies (Hippoboscidae: Ornithomyiinae) with the first European record of the African species *Ornithocona laticornis*. *Parasit. Vectors.* 17, 237. <https://doi.org/10.1186/s13071-024-06303-8>.
- Kolodziejek, J., Marinov, M., Kiss, B.J., Alexe, V., Nowotny, N., 2014. The complete sequence of a West Nile virus lineage 2 strain detected in a *Hyalomma marginatum marginatum* tick collected from a song thrush (*Turdus philomelos*) in eastern Romania in 2013 revealed closest genetic relationship to strain Volgograd 2007. *PLoS One* 9, e109905. <https://doi.org/10.1371/journal.pone.0109905>.
- Lamontellerie, M., 1965. Les tiques (Acarina, Ixodoidea) du sud-ouest de la France. *Ann. Parasitol. Hum. Comp.* 40, 87–100.
- Lindeborg, M., Barboutis, C., Ehrenborg, C., Fransson, T., Jaenson, T.G.T., Lindgren, P.E., Lundkvist, A., Nyström, F., Salaneck, E., Waldenström, J., Olsen, B., 2012. Migratory birds, ticks, and Crimean-Congo hemorrhagic fever virus. *Emerg. Infect. Dis.* 18, 2095–2097. <https://doi.org/10.3201/eid1812.120718>.
- Magano, S.R., Els, D.A., Chown, S.L., 2000. Feeding patterns of immature stages of *Hyalomma truncatum* and *Hyalomma marginatum rufipes* on different hosts. *Exp. Appl. Acarol.* 24, 301–313.
- Magyar, N., Kis, Z., Barabás, É., Nagy, A., Henczkó, J., Damjanova, I., Takács, M., Pályi, B., 2021. New geographical area on the map of Crimean-Congo hemorrhagic fever virus: first serological evidence in the Hungarian population. *Ticks Tick-Borne Dis.* 12, 101555. <https://doi.org/10.1016/j.ttbdis.2020.101555>.
- Mancuso, E., Toma, L., Pascucci, I., d'Alessio, S.G., Marini, V., Quaglia, M., Riello, S., Ferri, A., Spina, F., Serra, L., Goffredo, M., Monaco, F., 2022. Direct and indirect role of migratory birds in spreading CCHFV and WNV: a multidisciplinary study on three stop-over islands in Italy. *Pathogens.* 11, 1056. <https://doi.org/10.3390/pathogens11091056>.
- Marie-Angèle, P., Lommano, E., Humair, P.F., Douet, V., Rais, O., Schaad, M., Jenni, L., Gern, L., 2006. Prevalence of *Borrelia burgdorferi* sensu lato in ticks collected from migratory birds in Switzerland. *Appl. Env. Microbiol.* 72, 976–979. <https://doi.org/10.1128/AEM.72.1.976-979.2006>.
- Martyn, K.P., 1988. Provisional atlas of the ticks (Ixodoidea) of the British Isles.
- Matsumoto, K., Parola, P., Brouqui, P., Raouf, P., 2004. *Rickettsia aeschlimannii* in *Hyalomma* ticks from Corsica. *Eur. J. Clin. Microbiol. Infect. Dis. Off. Publ. Eur. Soc. Clin. Microbiol.* 23, 732–734. <https://doi.org/10.1007/s10096-004-1190-9>.
- Mehl, R., Michaelsen, J., Lid, G., 1984. Ticks (Acari, Ixodidae) on migratory birds in Norway. *Fauna Nor. B* 31 (1), 46–58.
- Menegon, M., Mancuso, E., Di Luca, M., Casale, F., Neves, L., Smit, A., Severini, F., Castelli, M., Di Giulio, A., d'Alessio, S.G., Goffredo, M., Monaco, F., Toma, L., 2024. *Amblyomma sparsum* Neumann 1899 on migratory birds from Africa: first records in Italy. *Ticks Tick-Borne Dis.* 15, 102387. <https://doi.org/10.1016/j.ttbdis.2024.102387>.
- Mihalca, A.D., Dumitrache, M.O., Magdaş, C., Gherman, C.M., Domşa, C., Mircean, V., Ghira, I.V., Pocora, V., Ionescu, D.T., Sikó Barabási, S., 2012. Synopsis of the hard ticks (Acari: ixodidae) of Romania with update on host associations and geographical distribution. *Exp. Appl. Acarol.* 58, 183–206.
- Molnár, E., 1982. Occurrence of tick-borne encephalitis and other arboviruses in Hungary. *Geogr. Med.* 12, 78–120.
- Németh, V., Oldal, M., Egyed, L., Gyurancsek, M., Erdélyi, K., Kvell, K., Kalvatchev, N., Zeller, H., Bányai, K., Jakab, F., 2013. Serologic evidence of Crimean-Congo hemorrhagic fever virus infection in Hungary. *Vector-Borne Zoon. Dis.* 13, 270–272. <https://doi.org/10.1089/vbz.2012.1011>.
- Norte, A.C., Ramos, J.A., Gern, L., Nuncio, M.S., Lopes de Carvalho, I., 2013. Birds as reservoirs for *Borrelia burgdorferi* s.l. in Western Europe: circulation of *B. turdi* and other genospecies in bird-tick cycles in Portugal. *Env. Microbiol.* 15, 386–397. <https://doi.org/10.1111/j.1462-2920.2012.02834.x>.
- Nowak-Chmura, M., Siuda, K., 2012. Ticks of Poland. Review of contemporary issues and latest research. *Ann. Parasitol.* 58, 125–155.
- Palomar, A.M., Portillo, A., Santibáñez, P., Mazuelas, D., Roncero, L., García-Álvarez, L., Santibáñez, S., Gutiérrez, Ó., Oteo, J.A., 2015. Detection of tick-borne *Anaplasma bovis*, *Anaplasma phagocytophilum* and *Anaplasma centrale* in Spain. *Med. Vet. Entomol.* 29, 349–353. <https://doi.org/10.1111/mve.12124>.
- Papadopoulos, B., Humair, P.F., Aeschlimann, A., Vaucher, C., Buttiker, W., 2002. Ticks on birds in Switzerland. *Acarologia* 42, 3–19.
- Papadopoulos, B., Morel, P.C., Aeschlimann, A., 1996. Ticks of domestic animals in the Macedonia region of Greece. *Vet. Parasitol.* 63, 25–40. [https://doi.org/10.1016/0304-4017\(95\)00877-2](https://doi.org/10.1016/0304-4017(95)00877-2).
- Pascucci, I., Di Domenico, M., Capobianco Dondona, G., Di Gennaro, A., Polci, A., Capobianco Dondona, A., Mancuso, E., Cammà, C., Savini, G., Cecere, J.G., Spina, F., Monaco, F., 2019. Assessing the role of migratory birds in the introduction of ticks and tick-borne pathogens from African countries: an Italian experience. *Ticks Tick-Borne Dis.* 10, 101272. <https://doi.org/10.1016/j.ttbdis.2019.101272>.
- Petney, T.N., Pfäffle, M.P., Skuballa, J.D., 2012. An annotated checklist of the ticks (Acari: ixodida) of Germany. *Syst. Appl. Acarol.* 17, 115–170.
- Pitó, A., Fedorov, D., Brlík, V., Kontschán, J., Keve, G., Sándor, A.D., Takács, N., Hornok, S., 2024. 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. *Curr. Res. Parasitol. Vector-Borne Dis.* 100201. <https://doi.org/10.1016/j.crpvbd.2024.100201>.
- Pomerantsev, B.I., 1959. Ixodid ticks (Ixodidae). *Am. Inst. Biol. Sci.*
- Rollins, R.E., Schaper, S., Kahlhofer, C., Frangoulidis, D., Strauß, A.F.T., Cardinale, M., Springer, A., Strube, C., Bakkes, D.K., Becker, N.S., Chitimia-Dobler, L., 2021. Ticks (Acari: ixodidae) on birds migrating to the island of Ponza, Italy, and the tick-borne pathogens they carry. *Ticks Tick-Borne Dis.* 12, 101590. <https://doi.org/10.1016/j.ttbdis.2020.101590>.
- Rubel, F., 2025. *Hyalomma aegyptium*: observed global distribution, imported specimens, preferred hosts and vector competence. *Ticks Tick-Borne Dis.* 16, 102438. <https://doi.org/10.1016/j.ttbdis.2025.102438>.
- Rudolf, I., Kejikova, R., Vojtisek, J., Mendel, J., Penazzi, K., Hubalek, Z., Sikutova, S., Estrada-Peña, A., 2021. Probable overwintering of adult *Hyalomma rufipes* in Central Europe. *Ticks Tick-Borne Dis.* 12, 101718. <https://doi.org/10.1016/j.ttbdis.2021.101718>.
- Saikk, P., Ulmanen, I., Brummer-Korvenkontio, M., 1971. Ticks (Ixodidae) on migratory birds in Finland. *Acta. Entomol. Fenn.* 28, 46–51.
- Sándor, A.D., Kalmár, Z., Matei, I., Ionică, A.M., Mărcuțan, I.D., 2017. Urban breeding corvids as disseminators of ticks and emerging tick-borne pathogens. *Vector Borne Zoonotic Dis. Larchmt. N* 17, 152–154. <https://doi.org/10.1089/vbz.2016.2054>.
- Sándor, A.D., Milchev, B., Takács, N., Kontschán, J., Szekeres, S., Hornok, S., 2021. Five ixodid tick species including two morphotypes of *Rhipicephalus turanicus* on nestlings of Eurasian eagle owl (*Bubo bubo*) from south-eastern Bulgaria. *Parasit. Vectors.* 14, 334. <https://doi.org/10.1186/s13071-021-04832-0>.
- Sándor, A.D., Péter, Á., Wong, J.B., Burri, R., Hornok, S., 2025. *Hyalomma rufipes* of Asian origin transported to Europe by a migrant bird. *Ticks. Tick. Borne Dis.* 16, 102518. <https://doi.org/10.1016/j.ttbdis.2025.102518>.

- Santos-Silva, M.M., Beati, L., Santos, A.S., De Sousa, R., Núncio, M.S., Melo, P., Santos-Reis, M., Fonseca, C., Formosinho, P., Vilela, C., Bacellar, F., 2011. The hard-tick fauna of mainland Portugal (Acari: ixodidae): an update on geographical distribution and known associations with hosts and pathogens. *Exp. Appl. Acarol.* 55, 85–121. <https://doi.org/10.1007/s10493-011-9440-x>.
- Santos-Silva, M.M., Sousa, R., Santos, A.S., Melo, P., Encarnação, V., Bacellar, F., 2006. Ticks parasitizing wild birds in Portugal: detection of *Rickettsia aeschlimannii*, *R. helvetica* and *R. massiliae*. *Exp. Appl. Acarol.* 39, 331–338. <https://doi.org/10.1007/s10493-006-9008-3>.
- Socolovschi, C., Reynaud, P., Kernif, T., Raoult, D., Parola, P., 2012. 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.* 3, 355–360. <https://doi.org/10.1016/j.ttbdis.2012.10.019>.
- Spengler, J.R., Estrada-Peña, A., 2018. Host preferences support the prominent role of *Hyalomma* ticks in the ecology of Crimean-Congo hemorrhagic fever. *PLoS Negl. Trop. Dis.* 12, e0006248. <https://doi.org/10.1371/journal.pntd.0006248>.
- Spengler, J.R., Estrada-Peña, A., Garrison, A.R., Schmaljohn, C., Spiropoulou, C.F., Bergeron, É., Bente, D.A., 2016. A chronological review of experimental infection studies of the role of wild animals and livestock in the maintenance and transmission of Crimean-Congo hemorrhagic fever virus. *Antivir. Res.* 135, 31–47. <https://doi.org/10.1016/j.antiviral.2016.09.013>.
- Toma, L., Mancini, F., Di Luca, M., Cecere, J.G., Bianchi, R., Khoury, C., Quarchioni, E., Manzia, F., Rezza, G., Ciervo, A., 2014. Detection of microbial agents in ticks collected from migratory birds in Central Italy. *Vector. Borne Zoonotic Dis.* 14 (199). <https://doi.org/10.1089/vbz.2013.1458>.
- Toma, L., Mancuso, E., d'Alessio, S.G., Menegon, M., Spina, F., Pascucci, I., Monaco, F., Goffredo, M., Di Luca, M., 2021. Tick species from Africa by migratory birds: a 3-year study in Italy. *Exp. Appl. Acarol.* 83, 147–164. <https://doi.org/10.1007/s10493-020-00573-4>.
- Turell, M.J., 2007. Role of ticks in the transmission of Crimean-Congo hemorrhagic fever virus. In: Ergonul, O., Whitehouse, C.A. (Eds.), *Crimean-Congo Hemorrhagic fever: a Global Perspective*. Springer, Dordrecht, Netherlands, pp. 143–154.
- Uiterwijk, M., Ibáñez-Justicia, A., van de Vossenbergh, B., Jacobs, F., Overgaauw, P., Nijse, R., Dabekausen, C., Stroo, A., Sprong, H., 2021. Imported *Hyalomma* ticks in the Netherlands 2018–2020. *Parasit. Vectors.* 14, 244. <https://doi.org/10.1186/s13071-021-04738-x>.
- Valcárcel, F., González, J., González, M.G., Sánchez, M., Tercero, J.M., Elhachimi, L., Carbonell, J.D., Olmeda, A.S., 2020. Comparative Ecology of *Hyalomma lusitanicum* and *Hyalomma marginatum* Koch, 1844 (Acarina: ixodidae). *Insects* (11), 303. <https://doi.org/10.3390/insects11050303>.
- Vial, L., Stachurski, F., Leblond, A., Huber, K., Vourc'h, G., René-Martellet, M., Desjardins, I., Balança, G., Grosbois, V., Pradier, S., Gély, M., Appelgren, A., Estrada-Peña, A., 2016. Strong evidence for the presence of the tick *hyalomma marginatum* Koch, 1844 in southern continental France. *Ticks Tick-Borne Dis.* 7, 1162–1167. <https://doi.org/10.1016/j.ttbdis.2016.08.002>.
- Wallménius, K., Barboutis, C., Fransson, T., Jaenson, T.G.T., Lindgren, P.E., Nystrom, F., Olsen, B., Salaneck, E., Nilsson, K., 2014. Spotted fever *Rickettsia* species in *Hyalomma* and *Ixodes* ticks infesting migratory birds in the European Mediterranean area. *Parasit. Vectors.* 7, 318. <https://doi.org/10.1186/1756-3305-7-318>.
- Wilhelmsson, P., Jaenson, T.G.T., Olsen, B., Waldenström, J., Lindgren, P.E., 2020. Migratory birds as disseminators of ticks and the tick-borne pathogens *Borrelia* bacteria and tick-borne encephalitis (TBE) virus: a seasonal study at Ottenby Bird Observatory in south-eastern Sweden. *Parasit. Vectors.* 13, 607. <https://doi.org/10.1186/s13071-020-04493-5>.
- Zeller, H.G., Cornet, J.P., Camicas, J.L., 1994. Experimental transmission of Crimean-Congo hemorrhagic fever virus by West African wild ground-feeding birds to *Hyalomma marginatum rufipes* ticks. *Am. J. Trop. Med. Hyg.* 50, 676–681.
- Zé-Zé, L., Nunes, C., Sousa, M., Sousa, R.de, Gomes, C., Santos, A.S., Alexandre, R.T., Amaro, F., Loza, T., Blanco, M., Alves, M.J., 2025. Fatal case of Crimean-Congo hemorrhagic fever, Portugal, 2024. *Emerg. Infect. Dis.* 31, 139–143. <https://doi.org/10.3201/eid3101.241264>.
- Zhou, R., Sprong, H., Liu, Q., Krafft, T., Estrada-Peña, A., 2025. Mapping the potential suitable habitats for *Hyalomma rufipes* (Acari: ixodidae) in Africa and Western Eurasia. *PLoS Negl. Trop. Dis.* 19, e0012923. <https://doi.org/10.1371/journal.pntd.0012923>.