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ABSTRACT

The eco-epidemiology of tick-borne diseases hinges on the abundance and distribution of hosts that sustain tick populations and the pathogens they carry. Research into the role of bird species in the feeding of *Ixodes ricinus* ticks, the primary tick species of veterinary and public health importance in Europe, remains scarce. This study endeavors to bridge these knowledge gaps by (i) assessing the density of feeding ticks (*DFT*) within a bird community to pinpoint species making substantial contributions, and (ii) exploring interannual variations in *DFT* over an extended timeline. Furthermore, we investigate whether variations in individual tick burden (*TB*) were more closely associated with the characteristics of bird species or interannual variations affecting the density of questing tick, using interannual *TB* variation as a surrogate. To fulfill these aims, we conducted a 13-year longitudinal study monitoring *I. ricinus* ticks feeding on a bird community in a periurban forest in France, covering breeding periods from 2007 to 2019. Within this community, we identified seven principal bird species significantly contributing to *I. ricinus* tick feeding: the Common Blackbird (*Turdus merula*), the Song Thrush (*Turdus philomelos*), the European Robin (*Erithacus rubecula*), the Dunnock (*Prunella modularis*), the Eurasian Blackcap (*Sylvia atricapilla*), the Great Tit (*Parus major*), and the Common Nightingale (*Luscinia megarhynchos*). Our results show that the bird community's contribution to tick feeding remained relatively consistent from year-to-year, though certain years displayed higher or lower *DFT* values related to the average over the study period. Moreover, five out the seven major species accounted for 80 % to 95 % of *DFT* annually. Consequently, we emphasized the need to broaden the scope of future research on bird contributions to tick population dynamics beyond merely thrushes (*Turdidae* species), to encompass a more diverse range of species, particularly those common birds that engage in ground foraging activities. Furthermore, variations in individual tick burden were predominantly influenced by the characteristics of bird species rather than by interannual variability in infestation rates. This finding suggests a significant role for species-specific traits in determining tick exposure and susceptibility. In conclusion, our study offers new insights into the medium-term dynamics of tick-bird ecological systems, underscoring the need for future study of tick populations and their interactions with vertebrate hosts to improve our understanding of tick-borne disease circulation.

1. Introduction

Ticks are one of the most important vectors of human pathogens, leading to an increase in public health problems worldwide (Rochlin and Toledo, 2020). In Europe, *Ixodes ricinus* is widespread and abundant in many countries, and is a vector of several pathogens causing diseases of medical and veterinary importance, including Lyme borreliosis, rickettsiosis, tick-borne encephalitis, babesiosis and anaplasmosis (Rochlin and Toledo, 2020; Semenza and Suk, 2018). This generalist tick feeds on >300 vertebrate host species, including mammals, birds and reptiles (Gern and Humair, 2002). *Ixodes ricinus* is exophilic and mostly found in forests and wooded areas, environments that are favorable to their development and the presence of a large number of vertebrate hosts (Hönig et al., 2019; Lebert et al., 2022). As the eco-epidemiology of tick-borne diseases (TBDs) depends on the abundance and distribution of hosts that can maintain tick populations and associated pathogens (Diuk-Wasser et al., 2020), identifying the groups of host species that are most important for feeding *I. ricinus* may help to guide the selection of host species to focus on in future studies (Perkins et al., 2003).

The density of feeding ticks (*DFT*) on a given host species population is defined as the total number of ticks of all life stages that have fed on this species for a given period (Rosà et al., 2007). This concept, under-used so far, is important to consider when identifying which host species contribute the most to maintain a tick population in an epidemiological system of interest (Hofmeester et al., 2016; Rosà et al., 2007). A proxy of *DFT* can be assessed on the basis of the product of the host-specific tick burden (average number of ticks per host) and the density of the given host species (Rosà et al., 2007). Hofmeester et al. (2016) used this approach by quantifying the relative contribution for 15 host species to feeding *I. ricinus* ticks at the European scale based on a systematic review of host-specific tick burden. The *DFT* by a given host may vary locally and temporally according to the seasonality of the questing tick density, the density of available hosts, and the trophic preferences of the ticks. For example, Rosà et al. (2007) observed that *DFT* followed temporal variations in rodent density.

Wild birds constitute a taxonomically and ecologically diverse component of the vertebrate fauna (Keve et al., 2022). The avian group with approximately 11,000 species, includes around 5000 species within the Passeriformes order (BirdLife International, 2022). Passerines exhibit a sedentary behavior during their breeding periods and inhabit a wide range of habitats that are suitable for ticks, including forests, wetlands or synanthropic environments (Dubska et al., 2011; König, 1968). These characteristics make birds significant contributors to the maintenance and local amplification of tick populations in environment in the vicinity of humans (Kocianova et al., 2017). Numerous species of passerine birds have been documented to host immature stages of *I. ricinus* ticks (Keve et al., 2022), with a tick burden varying significantly among avian species (Estrada-Pena et al., 2005; Heylen et al., 2017). This variability is attributed to specific life-history traits of birds, such as body mass, immune responses and vertical use of space (Ciebiera et al., 2019; Klaus et al., 2016; Marsot et al., 2012; Oorebeek and Kleindorfer, 2016), as well as seasonal variations (Kocianova et al., 2017) or habitat preferences (Parker et al., 2017). Although many studies have explored tick infestations in European bird species, the specific role of passerine bird species in tick-host interactions within European ecosystems is still not well understood (Rataud et al., 2021). Historically, most of these studies have concentrated on tick burdens during migratory periods (Battisti et al., 2020; Buczek et al., 2020; Jourdain et al., 2007), with relatively fewer exploring these interactions during the breeding season (Marsot et al., 2012). This breeding period, which extends from April to July in the Northern Hemisphere, represents the primary timeframe for assessing the role of birds in the local population dynamics of ticks, since both mainly reproduce during this season. Although some research has assessed the *DFT* within bird communities, these studies, on *Ixodes scapularis* ticks of North America (Battaly and Fish, 1993) or *I. ricinus* ticks in Europe, often span only one or two years, limiting our understanding of long-term patterns (James et al., 2011; Marsot et al., 2012). To our knowledge, no study has been conducted in Europe to comprehensively estimate which bird species contribute most significantly to the feeding of *I. ricinus* ticks at a local scale over an extended period of time (*i.e.* > 5 years).

To unravel the enduring role of avian population on tick dynamics, we conducted an extensive longitudinal monitoring study spanning 13 years (2007 to 2019). This investigation centered on the interactions between *I. ricinus* tick feeding and a breeding bird community located in a periurban forest in France. We integrated comprehensive analyses of temporal and interspecific variations in tick burden of birds. The overarching objectives of our study were (i) the identification of the key bird species within this community contributing significantly to tick feeding, based on *DFT* assessment, (ii) the scrutiny of annual fluctuations in *DFT* and, (iii) the assessment of whether the avian contribution to tick feeding was more closely associated to tick burden (*TB*) or bird density (*D*), both parameters defining *DFT*. Our hypotheses were formulated based on prior research concerning rodents and birds. First, we posited that *DFT* would exhibit substantial variations across bird species, with particular emphasis on the potential contribution to local tick population of other species than *Turdidae*, a family that is already renowned for its high tick burden. Second, we considered that a bird species characterized by a low *TB* but a high *D* might potentially feed more ticks than a species with a high *TB* but low *D*. Third, we anticipated significant interannual variations in the overall contribution of the bird community to tick feeding, driven by fluctuations in the availability of questing ticks and the densities of bird species. As elucidated earlier, numerous studies have underscored the influence of avian species and environmental conditions (or the sampling year as a proxy) on *TB* in birds. Building upon this understanding, we aimed to discern the principal determinant structuring individual *TB*. If avian species exerted a stronger influence on *TB*, it would suggest a prominent role for bird species-specific traits in shaping tick exposure and susceptibility. Conversely, a greater influence of the year would imply that extrinsic factors primarily drive individual TB, contingent on year-to-year variations in local environment conditions, including vegetation, meteorological fluctuations, or host species abundance, as these elements affect the questing density of ticks. We anticipated substantial inter-species variation in *TB* due to the effects of bird specific traits, as well as significant year-to-year variation in *TB* due to changes in questing tick densities. Additionally, in our pursuit of unraveling the mechanisms underpinning species-specific effect on *TB*, we sought to identify the specific avian traits of birds (species body mass and foraging height) associated with variation in *TB*.

2. Methods

2.1. Study site

The study site is situated approximately 22 km southeast of Paris, within the forest of Sénart, located in Essonne, France. Covering an area of 3200 hectares and positioned at coordinates 02°29′E longitude and 48°40′N latitude, 80 m above sea level. This forest receives >3 million visitors annually (Maresca, 2000), which has spurred research into acarological risk (Lejal et al., 2019). The forest primarily consists of broad-leaved trees, with oak species (*Quercus robur, Quercus petraea*) and European hornbeams (*Carpinus betulus*), dominating the landscape (Marmet, 2008). Our study plot was specifically located within the most open part of the forest, which was formerly used as sheep pastures and is now dominated by shrubs (dominated by *Prunus* sp. and *Crataegus* sp.). This area is surrounded by oak, hornbeam and aspen trees. The local avian community comprises various forest and shrubland bird species (Laury et al., 2007). The local breeding bird community was dominated by the Eurasian blackcap (*Sylvia atricapilla*), with 25.7 individuals per hectare on average, constituting 22.8 % of the captured birds. Other abundant species included the Common chiffchaff (*Phylloscopus collybita*), the Blue tit (*Cyanistes caeruleus*) and the European robin (*Erithacus*

rubecula), with average densities of 15.1, 13.9 and 11 birds per year and per hectare respectively, representing approximatively 13 %, 11.2 % and 10.1 % of captured birds (Table 1). Conversely, among the 13 considered species in the local breeding community over the study period, the Garden warbler (*Sylvia borin*) and the Marsh tit (*Poecile palustris*) were the least abundant, with respective average of 1.2 and 2.3 individuals per year and per hectare, comprising around 1 % and 1.9 % of the captured birds (Table 1).

2.2. Data collection

Birds were caught within a 4-ha square plot, using 14 vertical mist-nets (12-m long, 2.5-m high). These nets were spaced ~50 m apart, and were positioned to document the bird community inhabiting the local shrublands. Bird sampling was conducted from 2007 to 2019 during the breeding period of birds, from 1st May to 15th July, at a frequency of one morning capture session every two weeks ($n = 5$ sessions per year). For each captured bird, the species, the sex (male *versus* female *versus* unknown), the age (juvenile for those born during the spring of the year of capture *versus* adult), and the body mass were recorded. The number of ticks was counted on a subsample of captured birds (68.6 % of all captured birds) by one of us (PYH). Ticks were systematically counted when light was sufficient (*i.e.*, about 1 hour after dawn), when the number of captured birds was moderate (< ~10 birds per hour), and prioritizing less common species when too many birds were captured at the same time. Inspected birds were chosen independently of their apparent tick burden and of their individual traits. Ticks were counted only around the beak, where the majority of feeding ticks are generally found, as demonstrated in Marsot et al. (2012), and where counting is the most rapid and repeatable.

Ixodes ricinus is presumed to be the most prevalent tick species in our study, as it constitutes the predominant tick species observed on birds (Marsot et al., 2012) and rodents (Pisanu et al., 2010) within the studied forest. However, it is essential to note that the identification of tick species and stage in our study was made impossible by field constraints and to inherent challenges associated with systematically collecting and identifying tick species and stage hosted by birds over an extended period. Nevertheless, findings from a previous study conducted in the same forest by Marsot et al. (2012) indicate that all the hosted ticks were *I*. ricinus, of which 78 % were larvae while the remaining 22 % were nymphs.

2.3. Density of feeding ticks on birds (DFT)

Only bird species that had tick counts recorded for each year from 2007 to 2019 were included in the calculation of *DFT*. This selection encompassed a total of 2234 individuals from 13 different bird species (out of 36 bird species captured on the study plot). These selected species accounted for 91 % of all captured birds with recorded tick counts, representing 41 % of the bird species within the subsample. Remarkably, they hosted 96 % of all counted ticks in the bird community. Density of feeding ticks $DFT_{i,j}$ per bird species i and year j was calculated by multiplying the annual average tick burden of the bird species during the breeding period $TB_{i,j}$ by the estimated annual bird density during the breeding period $D_{i,j}$:

$$DFT_{i,j} = TB_{i,j} \times D_{i,j} \qquad (1)$$

The overall DFT_j of the bird community during the breeding period of the year j was estimated by summing the $DFT_{i,j}$ for all bird species i. As it is commonly assumed that the numbers of birds captured in mist-nets reflect local abundance (James et al., 2011), we also calculated *DFT* using the annual count of uniquely captured birds in the study area (*ACB*) instead of bird density *D*. This alternative calculation was undertaken to evaluate the robustness of our results in light of the inherent uncertainty associated with density estimates (see Appendix 1). This approach was justified by its applicability to a broader range of species, circumventing the need for complex density estimation, which typically necessitates capture-mark-recapture data of sufficient quality and

Table 1

Number of examined and infested bird individuals, mean density per hectare, prevalence of tick infestation, mean tick burden per examined and infested bird, mean foraging height (m) and mean body weight of adults (g) for 13 bird species of the bird community of the Sénart forest (France) during the breeding period between 2007 and 2019. [CI]$_{95\%}$ confidence interval at 95 % corresponded confidence interval at 95 % for proportion for Prevalence of infestation (prop.test function in R) and to non-parametric bootstrap intervals for mean D, TB and TB of infested birds (boot.ci function from package boot in R).

Bird species scientific name	Bird species common name	Number of examined birds	Number of infested birds	Mean D and [CI]$_{95\%}$	Prevalence of infestation (% and [CI]$_{95\%}$)	Mean TB and [CI]$_{95\%}$	Mean TB o infested bird and [CI]$_{95\%}$	Mean foraging height (m)	Mean body weight (g)
Aegithalos caudatus	Long-tailed tit	114	5	**9.4** [6.2 ; 12.6]	**4.4** [1.6; 10.4]	**0.1** [0.0; 0.1]	**1.2** [0.8; 1.6]	0.8	8.5
Cyanistes caeruleus	Blue tit	136	15	**13.9** [8.7 ; 19.0]	**11.0** [6.5; 17.8]	**0.1** [0.1; 0.2]	**1.1** [0.9; 1.4]	1.5	11.5
Erithacus rubecula	European robin	499	445	**11.0** [9.4 ; 12.6]	**89.2** [86.0; 91.7]	**5.5** [5.1; 5.9]	**6.1** [5.7; 6.6]	0.5	17.6
Luscinia megarhynchos	Common nightingale	111	87	**4.3** [3.5 ; 5.1]	**78.4** [69.4; 85.4]	**5.3** [4.1; 6.4]	**6.7** [5.4; 8.0]	0.3	20.1
Parus major	Great tit	234	122	**8.3** [5.9 ; 10.6]	**52.1** [45.5; 58.7]	**2.6** [2.0; 3.2]	**5.0** [4.0; 5.9]	2.6	18.2
Phylloscopus collybita	Common chiffchaff	298	74	**15.1** [12.1 ; 18.1]	**24.8** [20.1; 30.2]	**0.4** [0.3; 0.5]	**1.6** [1.4; 1.7]	1.3	7.7
Poecile palustris	Marsh tit	58	14	**2.3** [1.1 ; 3.6]	**24.1** [14.3; 37.5]	**0.4** [0.2; 0.6]	**1.5** [1.1; 1.9]	3.4	10.5
Prunella modularis	Dunnock	112	108	**4.7** [3.7 ; 5.8]	**96.4** [90.6; 98.8]	**9.3** [7.8; 10.8]	**9.6** [8.1; 11.2]	0.0	21.2
Pyrrhula pyrrhula	Eurasian bullfinch	67	28	**4.5** [2.7; 6.2]	**41.8** [30.1; 54.5]	**1.3** [0.5; 2.1]	**3.1** [1.4; 4.8]	2.5	31.0
Sylvia atricapilla	Eurasian blackcap	364	153	**25.7** [21.1 ; 30.4]	**42.0** [36.9; 47.3]	**1.4** [1.1; 1.7]	**3.3** [2.7; 4.0]	4.0	18.6
Sylvia borin	Garden warbler	117	18	**1.2** [1.0 ; 1.4]	**15.4** [9.6; 23.5]	**0.2** [0.1; 0.3]	**1.2** [0.9; 1.6]	1.4	18.7
Turdus merula	Common blackbird	75	75	**8.4** [5.5 ; 11.3]	**100** [100; 100]	**9.3** [6.8; 11.9]	**9.3** [6.6; 11.9]	1.0	97.0
Turdus philomelos	Song thrush	49	49	**5.6** [4.0 ; 7.3]	**100** [100; 100]	**7.9** [5.7; 10.0]	**7.9** [5.8; 10.0]	0.0	76.0
Total		**2234**	**1193**						

number.

2.4. Density of birds (D)

For analytical purposes, each session of bird capture was divided into 4 units (*i.e.*, 06:00–08:00 a.m., 08:00–10:00 a.m., 10:00 a.m.−12:00 p.m., 12:00–14:00 p.m.). As the number of recaptures was too low between two sessions of a year (Efford and Schofield, 2020) but sufficiently high within sessions, we used a spatially explicit capture-recapture model to estimate the bird density per hectare, for each species and at each session of each year (Efford et al., 2009). To estimate the proportion of individuals leaving the study site between subsequent sessions, we used a Cormack-Jolly-Seber (CJS) model to estimate the local survival probability (ϕ) of each bird species from one session to the following one (within the same year). We then calculated the annual density of each bird species by determining the number of new individuals per hectare that successively entered the study area per session, for each year. To do so, we first filled in for each species the missing values of estimated density from sessions without captured birds (20 % - it may happen that no individual of a species is caught during a session whereas the actual density is not zero) as follows: when the value of the first session of the year (session 1) was missing, we used the estimated density of birds of this species captured the next session. Similarly, if the value of the last session of the year (session 5) was missing, we used the value of the density estimated for the penultimate session. Also, if the values of the sessions 2, 3 or 4 were missing, we interpolated the value by averaging density estimates for the previous and subsequent sessions. Then, for each bird species i, the total number of birds per hectare $D_{i,j}$ for each year j was calculated as:

$$D_{i,j} = D1_{i,j} + \sum_{k=2}^{5} Dnew_{i,j,k} \tag{2}$$

with $D1_{i,j}$ the number of birds per hectare during the first session and $Dnew_{i,j,k}$ the number of new individuals at the session k. For a given session $k + 1$, if $D_{k+1} < D_k \times \phi_k$, $Dnew_{i,j,k}=0$; if $D_{k+1} > D_k \times \phi_k$, $Dnew_{k+1} = D_{k+1} - D_k \times \phi_k$.

2.5. Variation of DFT according to TB and D based on bootstrap analysis

To address our objective of assessing whether avian contributions to tick feeding were more strongly associated with tick burden *TB* or bird density *D*, both of which exhibiting variability across bird species and year-to-year fluctuations, we conducted a bootstrap analysis on *DFT*. To determine the relative influence of specific or inter-annual variability of *TB* or *D* on *DFT*, we recalculated $DFT_{i,j}$ for the bird community by substituting $TB_{i,j}$ or $D_{i,j}$ in formula (1) by $TB_{boot,j}$ or $D_{boot,j}$ respectively. First, for specific variability assessment, $TB_{i,j}$ and $D_{i,j}$ were re-estimated using a bootstrap procedure that randomly resample $TB_{i,j}$ or $D_{i,j}$ between species for each year. This approach allowed us to generate $DFT_{i,j}$ values under the assumption that $TB_{i,j}$ or $D_{i,j}$ were identical among species and could be considered interchangeable. Second, for inter-annual variability of *TB* or *D* on *DFT* assessment, $TB_{i,j}$ and $D_{i,j}$ were re-estimated using a bootstrap method that randomly resample $TB_{i,j}$ or $D_{i,j}$ between years for each species. This allowed us to generate $DFT_{i,j}$ values under the hypothesis that $TB_{i,j}$ or $D_{i,j}$ were identical among years and could be considered interchangeable. The bootstrap resampling was performed 100 times for each calculation of $DFT_{i,j}$. We considered that the further the observed $DFT_{i,j}$ of the bird community deviated from the distribution of bootstrapped $DFT_{i,j}$, the greater the influence of the bootstrapped parameter (specific and/or inter-annual variability of *D* and *T*) on structuring $DFT_{i,j}$.

2.6. Identification of determinants of bird tick burden

For the statistical analyses of *TB*, only the number of ticks recorded during the initial capture of a given year per bird was considered to avoid pseudoreplication. Due to the natural heterogeneity in parasite prevalence and infestation among host individuals (Mysterud et al., 2021; Newman et al., 2015), we ran zero-inflated negative binomial regression models (ZINB) (Venables and Ripley, 2002), using the number of ticks per individual bird as the response variable. Initially, we quantified the relative influence of interannual variation and interspecies variation on *TB* by estimating and comparing the coefficient of determination (denoted as R2, Zhang, 2018) from two ZINB models, including separately the effects of bird species and year. Subsequently, we conducted a single ZINB model combining the joint effects of bird species and year on *TB*. To account for individual bird characteristics, we included the variable sex/age in the model. Since birds in juvenile plumage are generally sexually monomorphic (sex not identifiable), age and sex were combined in a single variable sex/age, with three classes: juvenile *versus* adult male *versus* adult female. Results were reported as odds ratios (OR) along with their corresponding 95 % confidence intervals (CI). The European robin was chosen as the reference bird species since preliminary analyses indicated it had a TB most closely aligned with the median across all sampled species. As juveniles are absent early in the season, while both adults and juveniles are present later, the effect of age could be confounded by a seasonal effect (*e.g.* the later, the higher the abundance of ticks). To address the concern about the confounded effects of age and season, we re-assessed the age effect but using data from June and July only, when both age classes are exposed to the same abundance of ticks. We analysed this subsample of the data with the ZINB model described here before. We also assessed the strength of the seasonal effect on tick burden by fitting a ZINB model to adult data only (for the whole season), which included the joint effects of bird species, year and season on TB. In this model, the variable season is categorized into two groups: early season (April-May) and late season (June-July).

Finally, to verify former results on the main mechanisms underlying the interspecific differences in *TB* (Marsot et al., 2012), we studied the variation in *TB* according to two species-specific traits: the species mean body mass of adult birds captured during the period, and the species mean foraging height (H, in cm), as a proxy of vertical space use. As body mass and foraging height were weakly correlated (0.27), the effects of each covariate on *TB* were assessed with two univariate models. H was derived by calculating the percentage of foraging time spent across various vegetation layers, as per Wilman et al. (2014), and then weighting these percentages according to the significance attributed to each vegetation layer based on expert evaluations: $H = 5 * Fg + 100 * Fu + 400 * (Fm + Fc) \# (3)$ with *Fg* the percentage of time foraging on the ground, *Fu* below 2 m in understory of vegetation, *Fm* in mid to high levels (2 m upward, below canopy) and *Fc* in or just above canopy. The innovative aspect of our analysis, in addition to leveraging longitudinal data, lies in taking phylogenetic relatedness among species into account (Harvey and Pagel, 1991). We employed a univariate Markov Chain Monte Carlo algorithm (MCMCglmm R package version 2.32, Hadfield, 2010) to model the dependence of species-specific slopes for each influential variable on species traits. This approach accounted for the phylogenetic non-independence among species using pairwise phylogenetic uncertainty and slope uncertainty. Our analysis included a burn-in of 3000 iterations, during which posteriors were sampled at interval of 10 iterations. To address estimate uncertainty, species-specific slope estimates were weighted by their squared standard error, using the argument *mev* in the MCMCglmm function (Hadfield, 2010).

Data were analysed in R version 4.1.2 (R Core Team, 2020).

3. RESULTS

3.1. Density of feeding ticks on birds (DFT)

Tick counts showed that 53.4 % of birds were infested by ticks with an average tick burden of 3 ticks. Considering only infested birds, the mean burden was of 5.7 ticks per bird (Table 1). The most infested bird species were the Common blackbird (*Turdus merula*), the Song thrush (*Turdus philomelos*), the Dunnock (*Prunella modularis*) and the European robin, with a prevalence of infestation of 100 %, 100 %, 96.4 % and 89.2 % respectively, and a mean abundance of infestation of 9.3, 7.9, 9.2 and 5.5 ticks respectively (Table 1).

The contribution of the bird community to tick feeding exhibited relatively consistent patterns from one year to the next. While certain years displayed notably higher *DFT* values, than the overall average *DFT* for the entire study period (*DFT* = 315, see Fig. 1a), such as 2010 (*DFT* = 618), others, including 2008, 2013, and 2015 (with *DFT* values of 194, 203, and 216 respectively), recorded lower *DFT* values. Nevertheless, we did not observe any discernible temporal trend in these interannual variations.

We identified seven bird species contributing to feed 95 % of the ticks borne by the local breeding bird community: the Common blackbird

(25.7 %), the European robin (19.1 %), the Dunnock (13.6 %), the Song thrush (12.2 %), the Eurasian blackcap (11.5 %), the Great tit (*Parus major*, 6.6 %) and the Common nightingale (*Luscinia megarhynchos*, 6.6 %) (Fig. 1A and 1B). Moreover, only five of these species accounted for 80 % to 95 % of *DFT* each year. The six other species sampled: Long-tailed tit (*Aegithalos caudatus*), Blue tit (*Cyanistes caeruleus*), Common chiffchaff (*Phylloscopus collybita*), Marsh tit (*Poecile palustris*), Eurasian bullfinch (*Pyrrhula pyrrhula*), and Garden warbler (*Sylvia borin*) (referred as *Other species* in the Figures), accounted for <5 % of the local annual tick feeding over the study period (Fig. 1B).

Within the local bird community, the contributions to tick feeding (DFT) remained consistently stable over the period, with half of the community making almost no contribution at all. Among the seven bird species that were the most significant contributors to tick feeding, the extent of their contribution to DFT varied annually throughout the study period (Fig. 1A and 1C). For instance, the annual contribution of the Common blackbird fluctuated widely, ranging from 2 % to 70 %, and that of the Song thrush varied from 5 % to 40 % (Fig. 1A and 1C). Similarly, the European robin and the Dunnock showed moderate variation in their yearly contributions (Fig. 1A and 1C).

Considering the *DFT* per bird species, we showed a variability over time, with years of high and low tick production (Fig. 2A). As for the
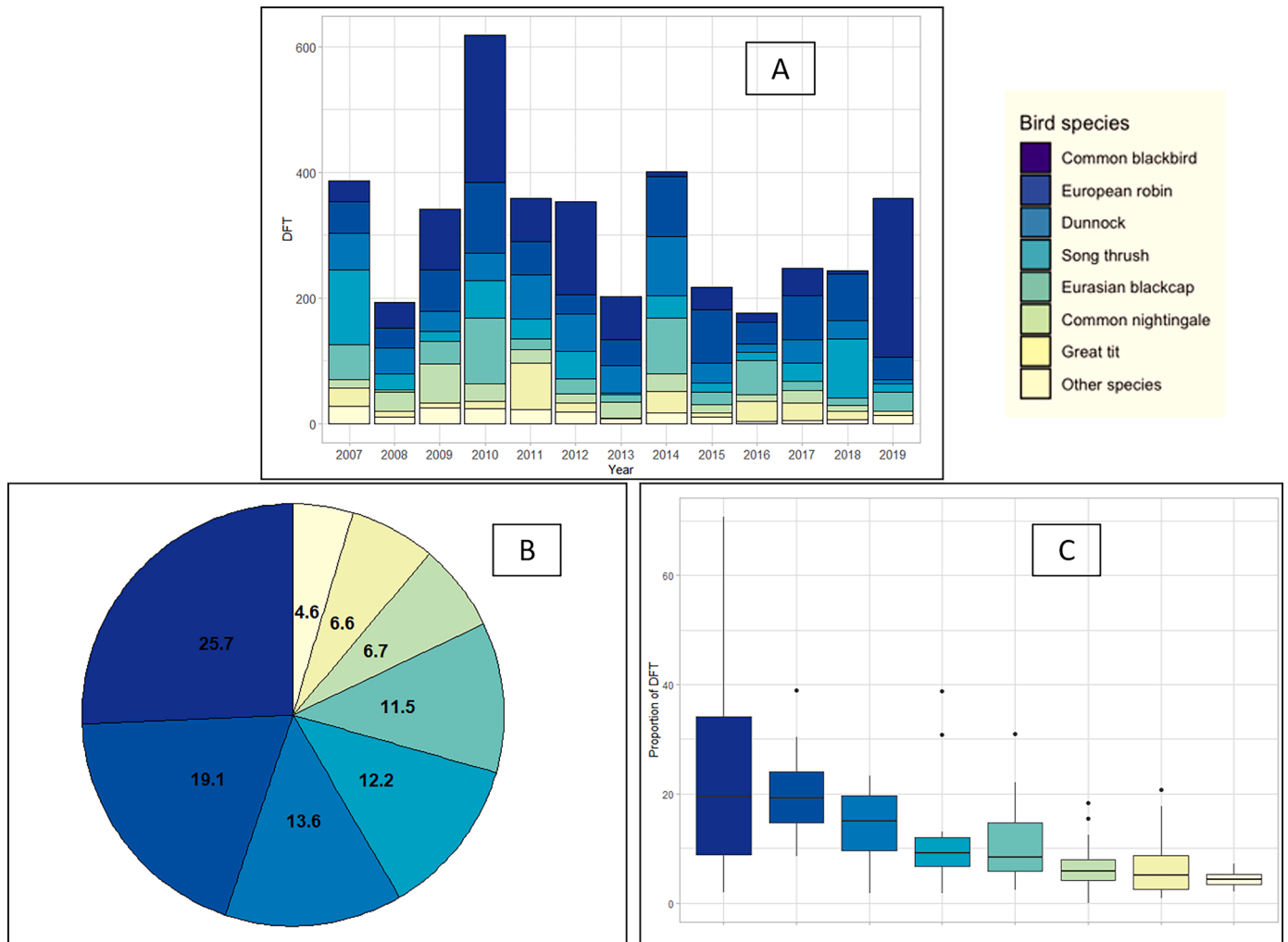

Fig. 1. Density of feeding ticks (DFT).
(A) Annual DFT of the bird community in the Sénart forest (France) (B) DFT per bird species during the study period for the seven main contributors to the local feeding of ticks (global contribution > 95 % between 2007 and 2019) and for the group of low contributors composed of six bird species (Other species), and (C) Annual distribution of the contribution to DFT by bird species during the study period, *i.e.*, the annual proportion of contribution to DFT by bird species relative to the total bird community contribution.
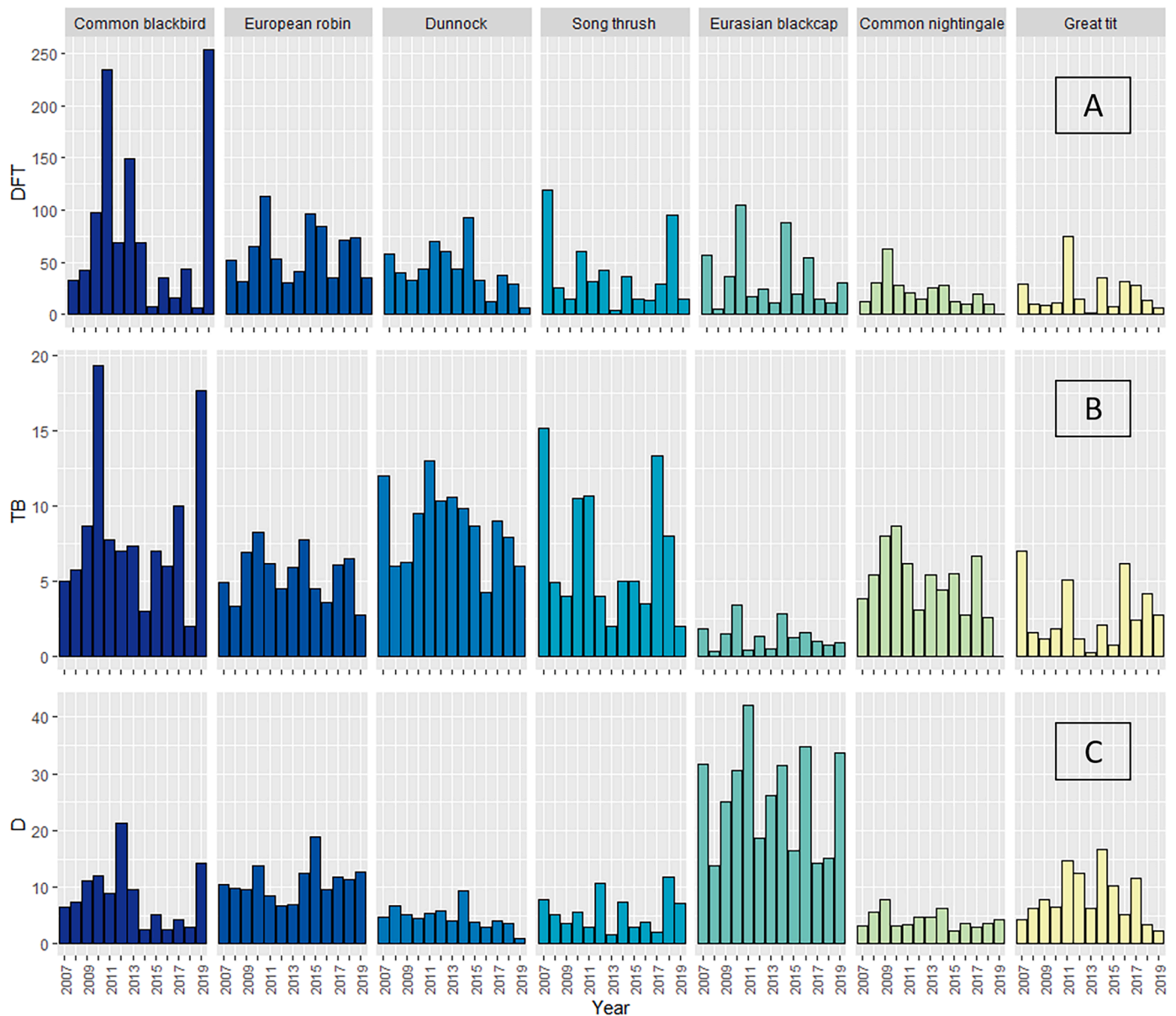
Fig. 2. Annual variation of (A) density of feeding ticks (DFT), (B) tick burden (TB) and, (C) bird density (D) for the seven main contributors to the local tick feeding in the bird community of the Sénart forest (France) during the breeding period.

overall *DFT* of the bird community, there was no temporal trend of interannual variations of specific *DFT*.

Regarding *DFT* drivers, our results highlighted that bird species with a high *DFT* were the species with a high *TB* (Common blackbird, European robin, Dunnock and Song thrush), with the exception of the Eurasian blackcap, which had a particularly high *D* and the European robin which had both high *D* and *TB* (Fig. 2, Appendix 2). Bird species with low *DFT* were species with low *TB* and variable *D*, such as the Long-tailed tit (*Aegithalos caudatus*) (Appendix 2).

DFT varied with *TB* and/or *D* across species and years. There was no specific relationship between *DFT* and its parameters *TB* and *D*. For example, the Common blackbird fed a high number of ticks in some years because of a high *TB* (2010 and 2019), or a high *D* (2012). Similarly, the Song thrush was a major contributor linked to a high *TB* in 2007 and to a medium *D* in 2018. Although *Turdidae* species were major contributors, years of low contribution from the Common blackbird (2007 and 2014) could still correspond to years of high tick feeding at the bird community level (Fig. 1a). Moreover, in years with low *DFT*, the Common blackbird could either feed many ticks (2013) or few ticks

(2018) (Fig. 1a). The regularity of the European robin's local contribution was linked to its consistently average *TB* and *D*, and that of the Dunnock to its consistently high *TB*. On the contrary, the European blackcap owed its contribution more to a high *D* than to a high *TB*.

Considering the local bird community, the bootstrap analysis showed that *DFT* fluctuations were predominantly influenced by the species-specific variation in both *D* and *TB* (Appendix 3A and 3C), rather than inter-annual variations in *D* and *TB* (Appendix 3B and 3D). Specifically, our finding revealed that when TB was considered, there were 2.5 times as many discrepancies between observed *DFT* and bootstrapped *DFT* values among species compared to those between years. Additionally, when focusing on D, the significance of the differences between observed *DFT* and bootstrapped *DFT* values among species surpassed the difference calculated between years by a factor of 3.7.

3.2. Determinants of tick burden

We noted that the *TB* of birds varied by year and bird species (Fig. 2). The coefficient of determination assessing the variation of *TB* of birds

among bird species was 0.88, while for interannual variation, it was 0.38. This suggests that individual *TB* variations were primarily influenced by bird species characteristics rather than fluctuations across years. The results from the ZINB model further supported these findings (Table 2). In the count component of the ZINB model, *TB* significantly differed among years. Birds hosted fewer ticks in 2019, while in 2007, 2010, 2011 and 2014, they hosted more ticks compared to 2013 (Table 2). However, the probability of belonging to the never-infested group of birds remained consistent across years in the zero-inflation component of the model (Table 2). Regarding the count model, the Eurasian bullfinch (*Pyrrhula pyrrhula*), the Eurasian blackcap, the Garden warbler, the Marsh tit, the Blue tit, and the Common chiffchaff exhibited lower *TB* compared to the European robin. Conversely, the Dunnock, the Song thrush, the Common blackbird and the Common nightingale had a higher *TB* values (Table 2). In the zero-inflation model, only the Long-tailed tit displayed a higher probability of being in the never-infested group of birds in comparison to the European robin (Table 2). Additionally, adult birds had lower *TB* than juveniles, and the likelihood of adult males and females belonging to the never-infested group was higher than that for juveniles (Table 2). But tick burden ($p = 0.013$) and occurrence ($p = 0.001$) were higher late in the season (June-July) than in early spring (April-May; tested with adults only), suggesting that the age effect could be partly confounded by a season effect. When analysing June-July data only, when both juveniles and adults are exposed to the same abundance of questing ticks, the effect of age remained a significant factor for tick counts, with adult birds having lower TB than juveniles (OR = 0.5 [95 % CI: 0.4; 0.6]; although this was non-significant for tick occurrence). Hence, we are confident with the conclusion that juveniles host a relatively larger load of ticks than adults. According to the MCMC models dealing with estimates from the

negative binomial part of the ZINB model, bird *TB* significantly increased with the species mean body mass (post mean = 0.04; IC = [0.01; 0.07]; p-value < 0.05) and significantly decreased with their mean foraging height (post mean = −0.7; IC = [−1.25; −0.12]; p-value < 0.05). Moreover, according to the MCMC models based on estimates from the zero-inflation part of the ZINB model, the probability that birds belong to the never-infested group of birds tended to decrease with the species mean body mass (post mean = −0.15; IC = [−0.43; 0.09]; p-value > 0.05) and tended to increase with the mean foraging height of birds, but results were not significant (post mean = 0.77; IC = [−0.38; 2.12]; p-value > 0.05). For the two components of the ZINB model, there was an interspecific similarity that can be explained by phylogenetic proximity, but this was only detected for the negative binomial part of the ZINB (which was also the most variable component between species).

4. Discussion

Quantifying the contribution of various vertebrate host species within a host community to feeding ticks, and identifying the most significant hosts are crucial steps to enhance our understanding of the tick population dynamics. While many studies have investigated the role of birds in the feeding of *I. ricinus* ticks, these have typically focused on tick burden estimates with data collected sporadically or over limited time frame and/or during migration period (Rataud et al., 2021). To our knowledge, our study represents the first comprehensive investigation conducted over an extensive temporal scale (13 years) during the breeding period, with the objective of estimating density of feeding ticks *DFT* and assessing its temporal variation within a bird community. Considering a community of 13 songbird species in France, we identified

Table 2

Estimates, odds ratio (OR, in bold), and their associated 95 % confidence intervals (CI) obtained from the ZINB model of the variation of tick burden of birds (TB) according to bird species, year and individual characteristics (sex/age) of the bird community in the Sénart forest between 2007 and 2019. Species and years have been ranked in the decreasing order of the estimates from the count component from the ZINB model.

Variable	Zero-inflation model (binomial with logit link)				Count model coefficients (negbin with log link)			
	Estimate (SE)	OR	95 % CI low	95 % CI high	Estimate (SE)	OR	95 % CI low	95 % CI high
Intercept	−5.4	–	–	–	1.6	–	–	–
Bird species								
European robin	–	–	–	–	–	–	–	–
Common blackbird	−16.3	**0.0**	0.0	+Inf	1.1	**2.9**	2.3	3.6
Dunnock	−0.7	**0.5**	0.0	118.0	1.1	**2.9**	2.4	3.5
Song thrush	−16.3	**0.0**	0.0	+Inf	0.9	**2.5**	1.9	3.3
Common nightingale	2.5	**11.7**	0.0	2865.5	0.5	**1.7**	1.4	2.1
Great tit	4.6	**99.8**	0.5	22,147.3	−0.2	**0.9**	0.7	1.0
Eurasian bullfinch	3.8	**47.6**	0.2	12,184.5	−0.5	**0.6**	0.4	0.9
Eurasian blackcap	4.4	**78.3**	0.4	17,525.2	−0.6	**0.5**	0.4	0.6
Common chiffchaff	4.7	**114.8**	0.5	28,618.7	−1.8	**0.2**	0.1	0.2
Long-tailed tit	7.6	**1922.2**	6.5	569,123.4	−1.9	**0.2**	0.0	1.5
Marsh tit	3.8	**43.2**	0.0	22,466.5	−2.6	**0.0**	0.0	0.2
Garden warbler	2.8	**16.4**	0.0	34,466.8	−2.6	**0.0**	0.0	0.2
Blue tit	2.7	**15.4**	0.0	1,902,539.0	−3.6	**0.0**	0.0	0.0
Sex/Age								
Juvenile	–	–	–	–	–	–	–	–
Adult female	0.8	**2.1**	1.1	4.2	−0.9	**0.4**	0.3	0.5
Adult male	1.3	**3.5**	2.0	6.4	−1.1	**0.3**	0.3	0.4
Year								
2013	–	–	–	–	–	–	–	–
2010	0.2	**1.2**	0.5	3.2	0.6	**1.8**	1.4	2.3
2011	0.9	**2.5**	0.9	6.7	0.4	**1.5**	1.1	1.9
2014	−0.3	**0.7**	0.2	2.3	0.4	**1.4**	1.1	1.9
2007	−0.2	**0.8**	0.2	3.0	0.3	**1.3**	1.0	1.7
2009	0.2	**1.2**	0.4	3.5	0.2	**1.2**	0.9	1.6
2012	0.2	**1.1**	0.4	3.2	0.1	**1.2**	0.9	1.5
2017	−0.6	**0.5**	0.2	1.9	0.2	**1.2**	0.9	1.5
2018	−0.4	**0.7**	0.2	2.7	0.2	**1.2**	0.9	1.5
2015	−0.3	**0.7**	0.2	2.5	0.0	**1.0**	0.8	1.3
2016	−1.2	**0.3**	0.0	1.6	−0.1	**1.0**	0.7	1.3
2008	0.3	**1.3**	0.4	4.0	−0.1	**0.9**	0.7	1.2
2019	−0.8	**0.4**	0.0	2.1	−0.4	**0.7**	0.5	0.9

seven major contributors to *I. ricinus* tick feeding. Our findings confirmed the observations that the *Turdidae* family, particularly the Common blackbird and the Song thrush, accounted for a substantial proportion of tick feeding on our study site over the entire period (38 %). This can be attributed to their consistently high infestation rates (Falchi et al., 2012; Gregoire et al., 2002; Marsot et al., 2012; Norte et al., 2012), despite not being the most abundant species of the community. Interestingly, we also showed that other bird species, including the European robin (*Erithacus rubecula*), the Dunnock (*Prunella modularis*), the Eurasian blackcap (*Sylvia atricapilla*), the Great tit (*Parus major*) and the Common nightingale (*Luscinia megarhynchos*), contributed significantly to tick feeding, collectively accounting for approximately 57 % of the *DFT* within the bird community. These findings underscore the importance of not exclusively focusing on *Turdidae* species in future studies investigating the contribution of birds to tick population dynamics, particularly since it has been shown that different species may have different reservoir status for pathogens such as *B. afzelii* (Gern et al., 1998). These results are preliminary and subject to confirmation by future field protocols. A larger dataset is necessary to evaluate the interaction between year and species more accurately (*i.e.*, to assess whether TB varies differently across years and species). However, increasing the number of birds captured per species per year is challenging, as we are constrained by their actual local population size (especially for species with low abundance). Additionally, increasing the number of sessions could lead to disturbances in the local population (Robinson, 2024; Robinson et al., 2009).In numerous studies evaluating the role of birds in tick feeding, particularly those involving captures of birds during breeding or post-breeding seasons, the Common blackbird and then the European robin have consistently emerged as the most common and noteworthy species contributing to tick production (Dubska et al., 2009; Estrada-Pena et al., 2005; Falchi et al., 2012; Klaus et al., 2016; Klitgaard et al., 2019; Movila et al., 2013; Norte et al., 2012; Wilhelmsson et al., 2020). Other bird species having a significant role in tick feeding varied among studies and, in most cases, only three to seven bird species were responsible for feeding nearly 80–90 % of ticks. This represents 8 to 19 % of the whole bird community on our study plot. Among these species, some notable contributors are similar to the ones identified in our study, such as the Song thrush, the Great tit, the Dunnock, the Eurasian blackcap, but some other species differ, such as the Eurasian wren, the Tree pipit and the Common chaffinch (Dubska et al., 2009; Estrada-Pena et al., 2005; Falchi et al., 2012; Klaus et al., 2016; Klitgaard et al., 2019; Movila et al., 2013; Norte et al., 2012; Rataud et al., 2022; Wilhelmsson et al., 2020). The Eurasian wren and Tree pipit were absent from our study plot, as both species tend to prefer respectively denser forested environments or more open woodland habitats. Although the Common chaffinch was present, it was captured in very limited numbers ranging from 0 to 2 individuals per year. Due to the absence or near absence of these species from our study site, we were unable to assess their contribution to tick feeding. The bird species in the studied community corresponded to species that are common and widely distributed in France. Indeed, 8 of the 13 considered species belong to the top 25 % most abundant common bird species in France (Fontaine et al., 2021; Julliard and Jiguet, 2002). Additionally, other common species in France may frequent forested tick habitats, but these species are not trappable by the implemented protocol as they do not frequent the ground and therefore do not play a role in tick feeding. Thus, it appears that the diversity of the bird community in our study could be comparable to that of bird communities in similar habitats across France.

It is most important to note that the contributions of bird species may exhibit spatial variations driven by local conditions influencing their densities. Additionally, these contributions may vary temporally, influenced by seasonal and annual factors, as demonstrated in our study. The contribution of the bird community to tick feeding exhibited relatively stable patterns from one year to the next, although there were occasional fluctuations, resulting in some years with higher or lower *DFT* than the

average over the entire study period. This observation contrasts with what has been reported in small mammals within woodlands ecosystems, as in Rosà et al. (2007). In our study, we found that interannual differences in the contribution of birds to tick feeding could vary by a factor of 2, while these variations reached a factor of 5 for rodents in the study of Rosà et al. (2007). This discrepancy suggests that interannual variation in *DFT* tend to be less pronounced for birds compared to rodents. This difference may be linked to the cyclic population dynamics observed in rodents, influenced by food resource availability (Andreassen et al., 2021), which does not occur in songbirds.

The studies evaluating the contribution of birds to tick feeding based their estimations on the number of birds captured, under the assumption that mist-net captures reflect local bird abundance (as commonly assumed in other studies, such as James et al., 2011). In contrast to these approaches, we estimated *DFT* using bird densities *D*, derived from estimates obtained with spatially explicit capture-recapture models. This approach enabled us to explore whether the identical ranking of bird species' contributions to local tick feeding could have been inferred using the annual count of captured birds (*ACB*) as a proxy of *D*. Upon comparing the estimations of *DFT* based on *D* and *ACB*, we found that the results were generally consistent, with the exception of the Song thrush (which exhibited lower *DFT* values based on *ACB* compared to *D*) and the Common nightingale (which showed higher *DFT* values based on *ACB* compared to *D*). These discrepancies were likely due to challenges in accurately estimating the densities of these bird species, stemming for small population sizes on the study site (particularly in the case of the Song thrush). For most species within the bird community studied, it appeared that using bird captures instead of density estimates to assess the role of birds in tick feeding represents a reasonable simplification. This result is important as it broadens the applicability of our approach to species with limited sample sizes, or to single-session sampling designs (that prevent estimating densities). Furthermore, this approach helps to bypass the intricate procedure of density estimation, which usually requires substantial amount of capture-mark-recapture data and suitable spatially-explicit capture-recapture models. In our situation, we resorted to an *ad hoc* method that combined session-specific density estimates and apparent survival rates across sessions, since a single model could not simultaneously estimate both parameters. Our study stands among the pioneering works that furnish evidence supporting the soundness of the use of *ACB* instead of *D* in this context. However, using *ACB* in the calculation of *DFT* should be interpreted with caution, especially for species with low population numbers, such as the Song thrush in our study. It should be noted that species among those contributing most to tick feeding (the Common blackbird, the Song thrush, and the European robin) showed a low correlation between *ACB* and *D*. Therefore, it is preferable to use *D* for these species. However, the results derived from *ACB* should be still qualitatively informative (but not quantitatively, as it does not correct for differences in capture probability between species).

Individual variations in tick burden were predominantly explained by the characteristics of bird species rather than by inter-annual variability of infestation, underscoring the significant role of species-specific traits in shaping tick exposure and susceptibility to infestation. Some species were consistently highly infested, while others rarely hosted ticks. In our study, the three primary tick carrier bird species were the Common blackbird, Song thrush, and Dunnock, aligning with findings from prior studies (as reviewed by Hofmeester et al., 2016). In our study, the Dunnock stands out as the most densely infested with ticks, normalizing the tick count on the Dunnock relative to its body mass underscores its predominance as a tick carrier. The Dunnock is known as one of the songbirds with the highest investment in sexual selection and spermatic competition (due to its polygynandrous mating system), which is generally associated with a down regulation of the allocation to immunity during the mating season (Davies and Hartley, 1996; Davies et al., 1996; Moller et al., 1999). This relatively low allocation to immunity in the Dunnock may explain it's particularly high tick burden (in

addition to its ground-foraging habit). Furthermore, the European robin, the Common nightingale and the Great tit have been identified as moderately infested tick species (Hofmeester et al., 2016). Our results confirmed that variations in tick burden among bird species can be attributed to specific traits, including foraging height: ground feeding birds are more exposed to ticks, and tend to exhibit higher infestation rates (as indicated by Ciebiera et al., 2019; Klaus et al., 2016; Marsot et al., 2012). Additionally, bird species with high body mass bear more ticks in line with previous studies (Marsot et al., 2012; Millien et al., 2023; Oorebeek and Kleindorfer, 2016), with wider avian species typically displaying higher infestation levels. Indeed, heavier birds often tend to be larger in size, exposing larger areas of skin suitable for tick attachment. This allometric relationship between tick burden and body size extends to rodents as well (Dallas et al., 2012; Harrison et al., 2010; Kiffner et al., 2011). We also highlighted an effect of age on tick burden, with adult males and females being less infested than juveniles. This effect is consistent with the results shown by Heylen et al. (2013) for female Great tit but differs from other studies (Gregoire et al., 2002; Scharf, 2004). It appears that the effect of age on bird tick burden is largely influenced by the species considered (relationship not assessed in our study) and these results must be interpreted with an understanding of the study period and the magnitude of the juveniles' age. Our findings suggest that the observed age effect on tick burden, with adults having lower *TB* than juveniles, might be influenced by differing exposure to tick stages. Specifically, adults are more likely exposed to nymphs during their peak activity in April-May, while juveniles, captured later in June-July, encounter more larvae. This potential confounding effect between tick stage and bird age highlights the need for future studies to differentiate between nymphs and larvae to better understand their respective impacts on tick burden. However, the higher tick occurrence and burden in juveniles than in adults must to be interpreted cautiously. Tick burden increased throughout the spring: the later in the season, the more birds are exposed to (or at least carry) ticks (demonstrated with adult data). And most juveniles fledge from the nest in late May to mid-June (Cuchot et al., 2024), *i.e.* relatively late in the spring. However, when considering only late-season data (*i.e.* after June 1st), the age effect on tick burden remained similar: adults carried less ticks than juveniles (though the proportion of birds carrying ticks no longer depended on age). To fully disentangle the effects of age and season, an advanced analysis of the non-linear effects of time on tick burden per age class and per species will be necessary. However, our sample size is currently insufficient for such an analysis. In our study, bird tick burden also varied between years (as in Elias et al., 2019; Gryczynska and Welc-Faleciak, 2016). This variation may be attributed to annual fluctuations in the density of host seeking ticks, as well as to changes in host populations (especially rodents, birds and cervids), which can affect the contact rate between birds and ticks (Bolzoni et al., 2012; Kiffner et al., 2011; Rosà et al., 2007). Further investigations is needed to comprehensively understand the inter-annual variations of this metric.

Our study offers insights into the complex ecology of ticks and underscores the need for ongoing monitoring of tick populations and their interactions with vertebrate hosts. For future studies at host community level, we recommend to involve both rodents and low-vegetation-stratum birds to enable a more precise delineation of their respective contributions to tick feeding dynamics. Additionally, extending the study by incorporating other key parameters influencing species-specific contributions to tick feeding, such as immunity, feeding success, and moulting success, would provide a more comprehensive understanding of the underlying complexities. Moreover, extending tick collection efforts throughout different months of the year would allow for the examination of seasonal variations in tick life stages and the production of questing nymphs. In doing so, we can better prepare for and mitigate the impact of the circulation of tick-borne diseases.

CRediT authorship contribution statement

Amalia Rataud: Writing – original draft, Formal analysis. **Alex Drouin:** Writing – review & editing, Writing – original draft, Validation, Software, Methodology, Formal analysis. **Laure Bournez:** Writing – review & editing, Validation, Conceptualization. **Benoit Pisanu:** Writing – review & editing, Validation, Software, Methodology. **Sara Moutailler:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition. **Pierre-Yves Henry:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization. **Maud Marsot:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Funding acquisition, Conceptualization.

Conflict of interest

The authors declare no conflict of interest.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ttbdis.2024.102390.

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