



HAL
open science

Research effort on birds' reservoir host potential for Lyme borreliosis: A systematic review and perspectives

Amalia Rataud, Pierre-Yves Henry, Sara Moutailler, Maud Marsot

► To cite this version:

Amalia Rataud, Pierre-Yves Henry, Sara Moutailler, Maud Marsot. Research effort on birds' reservoir host potential for Lyme borreliosis: A systematic review and perspectives. *Transboundary and emerging diseases*, 2021, 10.1111/tbed.14305 . anses-03330776

HAL Id: anses-03330776

<https://anses.hal.science/anses-03330776>

Submitted on 1 Sep 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Copyright

Research effort on birds' reservoir host potential for Lyme borreliosis: a systematic review and perspectives

Amalia Rataud^a, Pierre-Yves Henry^{b,c}, Sara Moutailler^d, Maud Marsot^{a*}

^a Université Paris Est, ANSES, Laboratory for Animal Health, Epidemiology Unit, Maisons-Alfort, France

^b Mécanismes adaptatifs et Evolution (MECADEV UMR 7179), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Brunoy, France

^c Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO), Centre d'Ecologie et des Sciences de la Conservation (CESCO UMR 7204), Muséum National d'Histoire Naturelle, Centre National de la Recherche Scientifique, Sorbonne Université, Paris, France

^d ANSES, INRAE, Ecole Nationale Vétérinaire d'Alfort, UMR BIPAR, Laboratoire de Santé Animale, Maisons-Alfort, F-94700, France

* Corresponding author: maud.marsot@anses.fr

Agence nationale de sécurité sanitaire de l'alimentation, de l'environnement et du travail

14 rue Pierre et Marie Curie 94701 Maisons-Alfort Cedex

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/tbed.14305](https://doi.org/10.1111/tbed.14305).

This article is protected by copyright. All rights reserved.

Abstract

Zoonotic tick-borne diseases threaten human and animal health. Understanding the role of hosts in the production of infected ticks in an epidemiological system is essential to be able to design effective measures to reduce the exposure of humans and animals to infectious tick bites. The reservoir host potential, *i.e.* number of infected ticks produced by a host species, depends on three components: tick production, realized reservoir competence and host density. The parameters and factors that determine the reservoir host potential need to be characterized to achieve a robust understanding of the dynamics of pathogen-tick-host systems, and thus to mitigate the acarological risk of emerging infections. Few studies have investigated the role of birds in the local spread of Lyme borreliosis *Borrelia*. Knowledge of the research effort on the reservoir host potential of birds in Lyme borreliosis *Borrelia* circulation is necessary to prioritize future research on this topic. We provide a systematic review of the research effort on components of the reservoir host potential of wild birds for Lyme borreliosis *Borrelia* circulation, and factors that modulate these components in the European epidemiological system. Our review of 242 selected publications showed that tick production has been 1.4 and 21 times more studied than realized reservoir competence and bird density respectively. Only one study achieved to characterize the global host reservoir potential of birds in a given epidemiological system. Investigated factors were mostly related to bird species identity, individual characteristics of birds and tick characteristics, whereas the influence of bird life-history traits have been largely under-investigated. Because simultaneous characterization of all parameters is notoriously complex, interdisciplinary research is needed to combine and accumulate independent field and laboratory investigations targeting each parameter on specific epidemiological system or host species. This can help gain an integrated appraisal of the functioning of the studied system at a local scale.

Keywords: reservoir host potential, wild bird, Lyme borreliosis, research effort

Introduction

Zoonotic vector-borne diseases constitute a serious threat to human and veterinary health at a global scale and represent one-third of the emerging infectious diseases in the last decades (De La Fuente et al., 2015; Estrada-Peña et al., 2014; Jones et al., 2008). Ticks are the second-most important vectors worldwide for diseases affecting humans (Toledo et al., 2009). They transmit a wide variety of infectious agents (bacteria, viruses and eukaryotic parasites) (Jongejan and Uilenberg, 2004) to many vertebrate host species including mammals, birds and reptiles (Sonenshine and Roe, 2013). Transmission of tick-borne diseases depends on both tick and host characteristics. These dependencies must be well understood to design effective measures to reduce exposure of humans and animals to infectious tick bites (Stanek et al., 2012; Tamzali, 2013). Involvement of ticks in the spread of tick-borne pathogens is determined by their ability to be infected by a pathogen, to harbour the pathogen and transmit it to a host during blood meal (vector competence) (McCoy and Boulanger, 2015). Moreover, hosts play an important role in the spread of tick-borne pathogens by being a food source for ticks – thereby participating in their population dynamics – and by their ability to acquire, harbour, replicate and transmit pathogens to ticks if they are competent reservoir hosts (Huang et al., 2019).

Brunner et al. (2008) described the reservoir potential of an individual host in tick-borne zoonotic cycles as the average number of infected ticks produced (fed, moulted and released into the environment) by an individual of a given host species. It is essential to understand the contribution of hosts in the production of infected ticks, because infected host-seeking nymphs in particular are a proxy of the risk for humans (*i.e.* acarological risk, McCoy and Boulanger, 2015). Here, we define the reservoir potential of a given host species population (reservoir host potential) which is based on three components (Fig. 1), *i.e.* two related to the host species population: (1) the number of ticks produced by the host species population (Tick production; Fig. 1, Table 1) (Brunner et al., 2008); (2)

the host species populations' ability to infect ticks (Realized reservoir competence; Fig. 1, Table 1) (Brunner et al., 2008), and one related to the environment of the host species population: (3) the host density at the local scale (Fig. 1, Table 1) (Giardina et al., 2000; Hofmeester et al., 2016; Huang et al., 2019; LoGiudice et al., 2003; Ostfeld et al., 2014; van Duijvendijk et al., 2015). Each host species population has its own reservoir host potential that acts in a specific context and thus can produce less or more ticks according to the site.

Characterizing the parameters that determine the reservoir host potential and the different host-intrinsic factors (individual host characteristics, host species, host life-history traits, host life period, etc.) and the host-extrinsic factors (weather conditions, habitat, tick biology, etc.) that influence these parameters in an epidemiological system can improve our basic understanding of pathogen-tick-host cycles, and our ability to mitigate the acarological risk. Moreover, understanding tick-borne infections must take into account the specificities of tick biology and the tick life cycle, e.g. hard ticks feed only once per life stage and are not infective until their blood meal in the next stage (Hartemink et al., 2008; Randolph and Craine, 1995). Knowledge on the actual research effort about the components and parameters that define birds' reservoir host potential is necessary to prioritize future research, and orientate it towards the least studied, but theoretically influential, components of such pathogen-tick-bird/mammal epidemiological systems.

Prior to reviewing the available literature on the topic, we have to define the fundamental components of a pathogen-tick-host system that ultimately determine reservoir host competence. This methodological framework structures the present work. The first component (tick production by a given host species population) is determined by four parameters. (1) Many studies have emphasized the importance of considering the number of ticks that feed on a given host (Tick burden; Fig. 1, Table 1) (Brisson and Dykhuizen, 2006; Brunner et al., 2008; Giardina et al., 2000; Hartemink et al., 2008; Hofmeester et al., 2016; Huang et al., 2019; LoGiudice et al., 2003; Ostfeld et al., 2014; Randolph and Craine, 1995; van Duijvendijk et al., 2015), which can be influenced by

various factors such as host behaviour, tick preferences, tick density and host attachment success (Brunner et al., 2008; van Duijvendijk et al., 2015). (2) The probability that ticks feed successfully (Tick feeding success: tick attachment success and blood meal success; Fig. 1, Table 1) determines the number of ticks produced by a host species population, and is influenced by tick host preferences, host behaviour (grooming), host immune response and duration of host attachment (Brunner et al., 2008; Hartemink et al., 2008). (3) The number of ticks produced by a host also depends on the probability that ticks successfully moult after blood meal (Tick moulting success; Fig. 1, Table 1), which can be influenced by both host species-specific factors and host immune response (Brunner et al., 2008; Huang et al., 2019; LoGiudice et al., 2003; van Duijvendijk et al., 2015). (4) A few studies have stressed the importance of documenting the survival probability (Fig. 1, Table 1) of ticks while they are attached on the host and once they are free in the environment (Hartemink et al., 2008; Randolph, 1998; Randolph and Craine, 1995).

The second component of the reservoir host potential of a given host species population (Realized reservoir competence) is determined by two main parameters: the pathogen's transmission from the tick to the host and the pathogen's acquisition from the host to the tick, which can be systemic or non-systemic (co-feeding). We are aware that these definitions are not always agreed upon within the research community, so we decided to keep Brunner's definitions that can be applicable on the field. Realized reservoir competence depends on: (1) prevalence (Host prevalence; Fig. 1, Table 1), *i.e.* the probability that the host is infected, which can be influenced by the force of infection (prevalence in nymphs, tick density, etc.) and host susceptibility to infection (Brunner et al., 2008; Hofmeester et al., 2016; van Duijvendijk et al., 2015) and (2) host infectivity (Fig. 1, Table 1), *i.e.* the probability that the infected host transmits the pathogen to the tick, which is influenced principally by both host immune response and duration of host infective period (Brunner et al., 2008; Giardina et al., 2000; Hartemink et al., 2008; Hofmeester et al., 2016; Randolph and Craine, 1995; van Duijvendijk et al., 2015). (3) The role of hosts in facilitating non-systemic transmission between co-

feeding ticks (Hartemink et al., 2008; Randolph and Craine, 1995) has been largely neglected, although it may play a non-negligible role because it can also contribute to the production of infected ticks. The influence of host traits operates here through the modulation of the propensity of ticks to aggregate and co-feed.

To well evaluate the reservoir host potential of a host species population at a local scale, all these parameters must be documented. However, some parameters are easier to assess (body tick burden, host prevalence) than others (tick feeding success, tick moulting success, tick survival, host infectivity, non-systemic transmission) (See Results section). Thus, the relative importance of these parameters in the estimation of reservoir host potential (by a sensitivity analysis) should be identified to help us to focus on the most important and the easiest to document.

Lyme borreliosis is a common infection of the temperate northern hemisphere (Kurtenbach et al., 2006) caused by spirochaetes belonging to the *Borrelia burgdorferi sensu lato* complex and transmitted by ticks of the family Ixodidae (Stanek et al., 2012). *Ixodes ricinus*, *I. persulcatus*, *I. scapularis* and *I. pacificus* are the main vectors of Lyme borreliosis in Europe, Asia, the north-eastern and the upper mid-western United States and the western United States, respectively (Stanek et al., 2012). They can feed on multiple host species (Oliver Jr, 1989). The main reservoir hosts for Lyme borreliosis *Borrelia* are small mammals, such as rodents, and some birds (Stanek et al., 2012). Many studies have investigated the reservoir host potential of small mammals in the spread of Lyme borreliosis *Borrelia* (Beckmann et al., 2019; Martello et al., 2019; Mysterud et al., 2019c; Pisanu et al., 2010). Exploring the reservoir host potential of wild birds has been under-investigated relative to rodents, although a complete understanding of the spread of Lyme borreliosis *Borrelia* must include wild birds because they can disseminate tick-borne pathogens over large distances during migration (Falchi et al., 2012; Klitgaard et al., 2019; Mysterud et al., 2019a), and can participate in the local dynamics of both ticks and tick-borne pathogens during their breeding periods (Marsot et al., 2012).

This brief introduction outlining the mechanisms linking pathogen, tick vector and host specificities in the acarological risk shows that they are well defined, but numerous, and seem to be difficult to document empirically (or worse, to quantify correctly). Many reviews of the literature have summarized the actual knowledge of the role of hosts in the of Lyme borreliosis *Borrelia* circulation. Some of them focused on the different reservoir hosts species that participate in the circulation of pathogens (Anderson, 1988, 1989; Gern, 2008; Gern et al., 1998; Hofmeester et al., 2016; Karbowiak et al., 2018; Magnarelli, 2011; Sala and De Faveri, 2016) and the different host species that could be infested by ticks (Castro and Wright, 2007; Evans et al., 2000; Jaenson et al., 1994). Others have studied more specifically the different birds hosting ticks (Bermúdez C et al., 2015; Evans et al., 2000; Gonzalez-Acuna et al., 2005; Kolonin, 2008; Loss et al., 2016; Sparagano et al., 2015) and those that could participate in the pathogens dynamics (Brinkerhoff et al., 2011; Comstedt et al., 2011; De La Fuente et al., 2015; Dietrich et al., 2011; Hasle, 2013; Hubalek, 2004; Humair, 2002; Loss et al., 2016; Reed et al., 2003). In addition to the state of the art on this information, knowledge on the actual research effort about the role of birds in the Lyme borreliosis *Borrelia* circulation is important to consider. The purpose of this literature-based systematic review was to determine which components of the reservoir host potential of wild birds for Lyme borreliosis have already been documented (or not), and how they have been measured. We therefore first present the parameters studied in this context around the world. Then we describe the different factors influencing these parameters specifically in the European epidemiological system. This allows us to identify which parameters are well documented in the scientific literature and those for which there is a lack of information.

Materials and methods

1. Literature search process

To identify the studies that potentially documented the reservoir host potential of birds in Lyme borreliosis *Borrelia* circulation, we followed the Preferred Reporting Items for Systematics Reviews and Meta-Analyses (PRISMA) statement (Liberati et al., 2009). All studies dealing with birds and *Ixodes* ticks and/or Lyme borreliosis were eligible for our systematic review. We conducted two electronic searches on 26 February 2020 on the Scopus and PubMed databases using the following search terms: (“*Ixodes*” AND “bird”) and (“bird” AND “*Borrelia*”). We used the “Article title, Abstract, Keywords” option to collect all papers in which the search terms appeared in the title, abstract or keywords. Information contained in papers was screened and extracted by the same person (AR). Papers were listed in EndNote software after removing duplicates.

2. Selection process

We selected studies based on the following inclusion criteria: journal articles and short communications written in English and focusing on the reservoir host potential of wild birds in the spread of Lyme borreliosis *Borrelia*, with no restriction on the publication date. Therefore, all studies on tick infestation in birds, *Borrelia* prevalence in birds, *Borrelia* prevalence in ticks collected while feeding on birds, bird infectivity, effects of birds on tick survival/attachment success/feeding success/moulting success were considered. The exclusion criteria included reviews, book chapters, notes and reports from congresses. Moreover, we kept only those studies focusing on wild birds and analysing host infectivity in experimental captive birds. We selected the studies following three steps: (1) by screening the title, excluding papers with titles irrelevant to the topic; (2) by screening the abstract to identify papers of legitimate interest and (3) reading the full text of the selected papers.

Appendix 1 provides the all the references included in the analysis.

3. Data collection process

Data were collected in a spreadsheet designed to systematically record the targeted information from the different studies. We qualitatively reported the parameters investigated in each paper to determine reservoir host potential of birds in the spread of Lyme borreliosis *Borrelia* (host density, host infestation by ticks, tick feeding success, tick moulting success, tick survival, host prevalence in *Borrelia*, host infectivity, non-systemic transmission), and the methods used to study them. Additional information related to the context of the study (study site, bird species, tick species, *Borrelia* species, bird period) was collected.

Supplementary Materials 2 provides the corresponding meta-dataset.

Results

1. Study selection

The searches on PubMed and Scopus returned 2 212 records. At the end of the selection process, 242 studies remained for the analysis (Fig. 2). The publication years dated from 1961 to 2019; of these studies, 23% were published before the 2000s and 77% after the 2000s and more than half of the studies (52%) were published after 2010. The relative publication rate on the topic (adjusted for the total number of publications in epidemiology per year) was stable across years (non-significant linear year effect, $LRT = 2.281$, $df = 1$, $P = 0.131$). Hereafter, research effort per topic is defined as the percentage of publications that addressed the given topic among the 242 analysed studies, or among a specifically defined subset of studies.

2. Parameters investigated to characterize the reservoir host potential of birds for Lyme borreliosis

The main parameters to be documented to characterize the reservoir host potential of birds for Lyme borreliosis at a local scale were defined above (see also Fig. 1, Table 1). Raw results presented hereafter are summarized in Figure 3.

Of the selected studies, 78% addressed the tick production component (Fig. 1, Table 1). Most of these studies investigated the tick burden parameter (93%), with 73% of them exploring the prevalence of infestation (% of infested birds), 34% exploring the mean abundance of infestation (mean number of ticks per total examined bird) and 32% exploring the mean intensity of infestation (mean number of ticks per total infested bird). Moreover, 8% of the studies addressing the tick production component investigated the tick-feeding success parameter, with 80% of them exploring tick attachment success on birds and 73% exploring blood meal success. Finally, 10% and 2% of the studies investigated respectively tick moulting success and tick survival parameters (Heffernan et al., 2014; Keesing et al., 2009; Levi et al., 2016; Wu et al., 2016).

More than half of the studies (57%) evaluated the realized reservoir competence component of birds (Fig. 1, Table 1): 28% of them investigated *Borrelia* prevalence in birds by using blood samples or skin biopsies of birds, 15% investigated bird infectivity, generally by carrying out xenodiagnoses (*i.e.*, by infesting the host with uninfected ticks in the laboratory, and demonstrating the presence of the pathogen in those ticks) and 3% investigated non-systemic transmission. Most of the studies exploring the realized reservoir competence of birds investigated *Borrelia* prevalence in ticks collected while feeding on birds (80%), which represents a proxy of bird prevalence, bird infectivity and non-systemic transmission.

Finally, only 4% of the studies addressed the bird density component (Fig. 1, Table 1) to understand the reservoir host potential of birds for Lyme borreliosis.

In addition, 4% of the studies attempted to characterize the global reservoir host potential of birds by analysing the blood-meal remnant of host-seeking ticks.

More than half of the studies (56%) simultaneously assessed at least two different parameters: 36% of the studies investigated both tick burden and *Borrelia* prevalence in ticks collected while feeding on birds. Tick burden was also investigated in combination with *Borrelia* prevalence in birds (9% of the studies), bird density (3% of the studies) and bird infectivity (3% of the studies). Bird infectivity was investigated slightly more often with *Borrelia* prevalence in feeding ticks (3% of the studies) than with bird density (1% of the studies) (Giardina et al., 2000; Keesing et al., 2009; Levi et al., 2016) and bird prevalence (1% of the studies) (Humair et al., 1998; Levi et al., 2016; Norte et al., 2013). Only the Levi et al. (2016) study investigated all parameters in the same system to develop a model focusing on the within-season dynamics of the Lyme borreliosis agent circulating in vertebrate populations (including birds) in the north-eastern USA.

Results are summarized in Figure 3 and Appendix 2.

3. Focus on the European epidemiological system

Raw results presented hereafter are summarized Figure 4 and Appendix 3. The majority of studies (49%) addressed the European epidemiological system, which is composed principally of *B. garinii*, *B. valaisiana*, *B. afzelii*, *B. turdi*, *Ixodes* spp. ticks (mainly *I. ricinus*) and Palearctic birds. The second most studied epidemiological system was North America (35% of studies), followed by a small number of studies in the other parts of the world: 6% in Asia, 5% in South America, 3% in Africa and 3% in Oceania. The goal of this third part of the literature review was to report on the research effort on the different factors that influence reservoir host potential. Because the factors depend on the studied epidemiological system (in contrast to the parameters that are specific to the global epidemiological model and, consequently, applicable worldwide), we focused on one single system, the European epidemiological system (based on 118 studies).

Among the European studies, 69% addressed the tick production component (Fig. 1, Table 1), with most focusing on the tick burden parameter (91%). The main factors studied that may influence tick

burden in birds were host-intrinsic factors, such as bird species identity (65% of the European studies focusing on tick burden), bird age (20%), bird foraging height (19%), bird sex (14%) and host-extrinsic factors such as tick life stage (43%), tick species (28%), seasonal variation (22%), between-site variation (16%) and inter-annual variation (14%).

Among the European studies, 58% addressed the realized reservoir competence component of birds (Fig. 1, Table 1). Of these studies, 29% focused on the *Borrelia* prevalence in birds parameter and mostly investigated the influence of host-intrinsic factors, such as bird species identity (45%), bird sex (20%) and bird age (15%). The most investigated host-extrinsic factor was the site (20%). Among the European studies exploring the realized reservoir competence component, 16% focused on bird the infectivity parameter by investigating, for the most part, the influence of *Borrelia* species identity (36%) and tick species identity (18%). Finally, 72% of the European studies focused on the *Borrelia* prevalence in ticks collected while feeding on birds (proxy of *Borrelia* prevalence in birds, bird infectivity and non-systemic transmission); they generally investigated the influence of host-intrinsic factors, such as bird species (70%) and host-extrinsic factors such as tick life stage (48%), *Borrelia* species (32%), tick species (24%), seasonal variation (14%) and between-site variation (10%).

Most studies focused on land birds (83%, corresponding to a positive bias in investigation effort in favour of this group, being over-represented by a factor of 1.7 relative to the proportion of land birds among Palearctic bird species, based on <https://avibase.bsc-eoc.org/checklist.jsp?region=EUC>, checked on 20 September 2020). These studies mostly examined passerines, especially the genus *Turdus* (63% of all studies), followed by *Erithacus* sp. (54% of the studies), *Parus* spp. (50% of the studies), *Sylvia* spp. (45% of the studies) and *Fringilla* spp. (41% of the studies). Studies also dealt with game birds (11%; positive bias: over-representation of 2.6), marine birds (8%; negative bias: under-representation of 1.4), birds of prey (4%; negative bias: under-representation of 2.5) and waterfowl (3%; negative bias: under-representation of 8.8).

A total of 57% of the European studies mentioned the stage of the annual cycle of birds: 59% of the studies relied on data collected during the migration period (equally spread between autumn and spring migration, respectively 55% and 53%), 46% addressed the breeding period, and 6% addressed the winter period.

Results are summarized Figure 4 and Appendix 3.

Discussion

To properly understand how a given epidemiological system works, the three components that define the overall reservoir host potential of a host species population should be measured (Fig. 1, Table 1). However, such an integrated characterization of a pathogen-tick-host system is so difficult that only one single study came close to accomplishing this feat to date (Levi et al., 2016). The goal of this study was to determine how changes in the vertebrate community composition could influence the density of *Borrelia* infected nymphs (acarological risk). Thanks to long-term field data, they first explored the degree of larvae redistribution on individual host when host densities vary. Then, they implemented a model to describe the transition from questing larvae to infected or uninfected nymphs according to data based on host densities, post-grooming body tick burden, feeding survival and realized reservoir competence, which are all the components of the reservoir host potential.

A more feasible approach is to split the investigation into several studies, each addressing one or a few components and/or parameters of the epidemiological system, independently from the others. Several literature surveys have provided updated overviews of available knowledge about the reservoir host potential of birds in the Lyme borreliosis *Borrelia* circulation (Bermúdez C et al., 2015; Brinkerhoff et al., 2011; Comstedt et al., 2011; De La Fuente et al., 2015; Evans et al., 2000; Gonzalez-Acuna et al., 2005; Hasle, 2013; Hubalek, 2004; Humair, 2002; Kolonin, 2008; Loss et al.,

2016; Reed et al., 2003; Sparagano et al., 2015). These reviews particularly addressed the role of different bird species in ticks or pathogens dynamics. To our knowledge, none of them had provided a comprehensive analysis of the existing research effort on this topic, at least not by systematically analysing the research coverage for each component and parameters of the reservoir host potential of birds for Lyme borreliosis (Fig. 1, Table 1). This was the goal of the present review.

Tick production was the most studied component (Fig. 3 and Appendix 2) and was mainly investigated by exploring the tick burden in birds (Tick burden; Fig. 1, Table 1). This parameter was generally assessed quantitatively by characterizing the prevalence of infestation, the mean abundance of infestation and/or the mean intensity of infestation, likely because these measurements are relatively easy to carry out in the field (*i.e.* count of feeding ticks on captured birds). This parameter is important to consider because it indicates the number of ticks fed by the host, which determines the tick production component (Fig. 1, Table 1). The importance of this parameter, and its relatively easy documentation in the field, make us recommend to continue its documentation in varied habitats-birds-tick-systems, to gain a robust understanding of the variability of *Borrelia's* eco-epidemiological systems. Among the parameters for tick production, tick moulting success, tick feeding success and tick survival parameters were respectively 9, 11 and 44 times less frequently studied than tick burden, illustrating the difficulty of investigating them. As these parameters determine the proportion of host seeking ticks in the next stage after their blood meal on the host, they are really important to document because they provide information on the actual tick production by hosts in a multi-host system.

Realized reservoir competence (Fig. 1, Table 1) was the second-most studied component (but 1.4 times less than tick production: Fig. 3 and Appendix 2), and was mainly investigated by exploring the *Borrelia* prevalence in ticks collected while feeding on birds, probably because it is the most easily documented parameter by field ornithologists. 96% of studies on *Borrelia* prevalence identified and accounted for the developmental stage of sample feeding ticks (*i.e.* larva, nymph or

adult), which is very important. Host-seeking tick larvae are *Borrelia*-naïve (Richter et al., 2012) and can become infected with *Borrelia* spp. only if they feed on an infected and competent host during their first blood meal (apart from non-systemic transmission through co-feeding). Infected feeding larvae are likely to have been infected *via* their (single) feeding host; in contrast, infected feeding nymphs may have been infected during their previous blood meal as larvae, and are therefore uninformative about realized reservoir competence of the host on which they are collected. Therefore, *Borrelia* prevalence in bird-feeding larvae (and only larvae) is a reliable proxy of bird infectivity and bird prevalence (for infective birds). However, *Borrelia* prevalence cannot separate systemic (bird infectivity) from non-systemic (co-feeding) transmission and is a proxy of the overall tick-borne *Borrelia* transmission *via* birds. Thus, *Borrelia* transmission *via* birds to feeding larvae is a key parameter for the assessment of the acarological risk at a local scale. In effect, successful feeding larvae that become infected and that successfully survive and moult into the nymphal stage will become infected host-seeking nymphs, which can transmit *Borrelia* to future hosts. *Borrelia* prevalence in host-feeding larvae allows us estimating the global realized reservoir competence of a given host species population and factors that could influence it should be studied with a specific interest to identify birds which can produce infected larvae. We must continue to investigate realized reservoir competence, but for an increasing diversity of *Borrelia*-ticks-birds systems, and with a specific effort to simultaneously document both tick burden and birds densities (as exemplified in Stafford et al., 1995) to identify bird host species that predominantly spread Lyme borreliosis *Borrelia* in multi-host systems.

Among selected studies, bird density (Fig. 1, Table 1) was the least studied component (4% of the studies, Fig. 3 and Appendix 2). In bird communities, tens of species can co-occur in the same eco-epidemiological system and differ in density - a few are abundant, and most occur in limited numbers (Marsot et al., 2012). Because bird species differ in tick production and in realized reservoir competence, ignoring differences in host availability prevents a global understanding of

epidemiological systems that involve multiple host species. For example, a high-density host species population, with moderate tick production and/or realized reservoir competence components, may participate more in the acarological risk than a low-density host species population with high tick production and/or realized reservoir competence components. We noticed that this latter component was very little studied in the context of Lyme borreliosis epidemiology, whereas the ornithological community can provide counts of birds at large spatial and temporal scales for nearly all existing species - for example, when we searched for “bird” AND “density”, 10144 results appeared in PubMed and 17561 in Scopus databases; (Jiguet et al., 2012; Schmeller et al., 2012). This means that, since only 4% of former studies documented bird host density, the vast majority of the knowledge we have cannot be used to infer the contribution of birds to Lyme borreliosis dynamics. We warmly recommend more interdisciplinary collaboration and data sharing between epidemiology and ecology scientists to fill this gap: methods and data for bird density already exist - at a low cost, (Levrel et al., 2010)-, they just need to be used.

Only 4% of the studies characterized the reservoir host potential by analysing the blood-meal remnant of host-seeking nymphs. This approach provides precious information on the overall reservoir host potential by identifying the host species on which the tick has fed during its previous blood meal as a larva, along with associated pathogens. Blood-meal remnants can help bypass the estimation of each component defining the reservoir host potential of a host species population and directly provide information on the proportion of hosts that successfully feed and infect ticks during their larval stage. However, this method suffers from a non-negligible rate of ‘false negative’ (only 31% of successful host species identification, Marsot et al., unpublished work). More importantly, the successful identification of the former host may depend on species traits (e.g. immunity, class – contrary to mammals, avian and reptilian erythrocytes contain a nucleus, and provide much more DNA), what can yield a highly biased representation of hosts that participate in the acarological risk.

In the European study selection, the most frequently studied factors determining reservoir host potential were host-intrinsic factors (Fig. 3 and Appendix 3), and more specifically the bird species and individual host characteristics (age and sex). These factors are essential in any exploration carried out to better understand pathogen-tick-host cycles and how they can ultimately influence acarological risk. However, other poorly studied host-intrinsic factors may be even more influential, such as species life-history traits (in particular: nest site, foraging height, immunity), that influence both tick production (Heylen et al., 2013; Marsot et al., 2012), and host reservoir competence -higher in species with a fast pace of life (Ostfeld et al., 2014). Among these species' traits, foraging height was the most investigated (e.g., 74% of the European studies investigating the impact of species life-history traits factors on tick burden of birds).

Among explored host-extrinsic factors (Fig. 3 and Appendix 3), the most investigated ones were mainly tick traits (species, life stage). Infected generalist ticks can more strongly enhance the acarological risk, because they can feed on multiple host species and thus be infected or infect them, than specialist ticks that feed on a restricted panel of hosts. Tick species and particularly associated host preferences (multi-host generalist vs. oligo-host specialist), should be investigated in combination with pathogen factors (*Borrelia* species) to understand how they interact. For example, pathogens borne by ornithophilic ticks (such as *I. arboricola* and *I. frontalis* in Europe) may be bridged by generalist ticks (such as *I. ricinus* in Europe) to other hosts in the epidemiological system (Heylen et al., 2014; Heylen et al., 2017). This highlights the importance of also paying attention to which tick species feed on birds. Moreover, site, habitat and climatic conditions were little studied although they are important host-extrinsic factors to consider because they can influence both local tick density populations and pathogen dynamics, and therefore reservoir host potential. Approaches accounting climate/habitat differences between sites should largely improve the quality of Lyme borreliosis risk prediction.

Existing studies proved to be highly biased in terms of bird phylogenetic coverage. 83% addressed ticks borne by common land birds, especially passerines. Birds of prey and waterfowl were the most understudied (relative to the number of species per Palearctic bird families) possibly because of their low exposure to ticks due to their behaviour or habitat. Efforts should be made to obtain representative samples of tick burden, realized reservoir competence parameters and host density for a broader range of bird species, and at least for some large land birds (Colombidae, Gallinaceae) and waterfowl birds (Rallidae, Anatidae). Pigeons, turtles, mallards, feral geese, coots now commonly dwell in urban areas, and some of them frequently commute between urban green spaces and rural agricultural lands or waterbodies. These groups could be of particular interest to understand the currently increasing acarological risk in suburban areas (Heylen et al., 2019).

Although there are exchanges of *Borrelia* spp. between marine and terrestrial enzootic cycles (Gómez-Díaz et al., 2011), the involvement of marine birds in the Lyme borreliosis acarological risk seems to be weak, because the ticks feeding on marine birds are specialists (*I. uriae*) and are unlikely to infect other competent hosts such as small mammals or humans.

Finally, most studies on bird-borne ticks focused on birds during migration. The distinct periods in the annual life cycle of bird hosts is important to consider because they constrain the inferences that can be made about realized reservoir competence. First, migratory birds are obvious ideal agents for long-distance dispersal of ticks and pathogens (Mysterud et al., 2019b). However, during migration time (fall and early spring), tick activity is very limited (Kurtenbach et al., 2006). Hence birds can transport pathogens, but they can only infect and produce only a limited number of ticks, at least much more limited than during the reproductive period, when both hosts and ticks multiply. Late summer/autumn is indeed the period of the year with the highest density of bird hosts (numbers of juveniles and adults are at their maximum, just after reproduction and prior to winter mortality), and thus corresponds to the maximum transmission period. The breeding period is also to key to understand because it corresponds to the sedentary time for birds (birds are settled on

their breeding grounds for some months), which overlaps with the activity peak of ticks -especially *I. ricinus*, the main vector of Lyme borreliosis in Europe (Stanek et al., 2012). This overlap means that, during the breeding season, birds contribute to a greater extent to the local circulation of ticks and associated *Borrelia* (Heylen et al., 2013; Marsot et al., 2012). Moreover, the bird breeding period occurs in spring, the season during which humans participate in outdoor activities that expose them to tick bites and therefore to *Borrelia* infection. Eventually, winter is not a favourable time for exophilic ticks and many migratory birds are absent from temperate zone systems. However, investigations during this period are still relevant because some tick species primarily feed on birds during winter (Agoulon et al., 2019).

Overall, we recommend to continue documenting as many systems as possible, particularly to increase the quantity of information for the least studied components of birds host reservoir potential (Fig 1, i. e. mainly tick moulting success, tick feeding success, tick survival, bird density), and to better cover the diversity of birds life history traits. However, we acknowledge that “doing as much as possible” is a poor strategy, of limited interest when it comes to prioritizing future research effort. In complement to the present assessment of past research effort, and available estimates for documented parameters, we now need sensitivity analyses of mathematical models of *Borrelia*-ticks-birds systems. Sensitivity analyses will identify the relative contribution of the different parameters to the global reservoir host potential (Dunn et al., 2013). It is this theoretical exercise that will allow distinguishing i) poorly documented parameters that are likely to be among the most influential – eventually achieving the measure of these parameters (and their variability) is of primary importance, ii) from poorly documented parameters that are unlikely to be key in the outbreak of *Borrelia* – and these parameters would not deserve much research effort, particularly given that, if they have been under-investigated until now, they must be costly or difficult to measure. To our knowledge, such a mathematical exploratory sensitivity analysis does not exist yet for the reservoir host potential of birds in the Lyme borreliosis *Borrelia* circulation.

Conclusions

By documenting the research effort on the components and factors that define the reservoir host potential of birds for Lyme borreliosis, we showed that very few studies have simultaneously addressed all the main parameters probably due to the difficulty of carrying out such an integrative study. Only one study has successfully developed a model integrating all the parameters of reservoir host potential (Levi et al. 2016). Characterizing all the parameters at the same time is complex; alternatively, combining and accumulating independent field and laboratory investigations targeting each individual parameter on a specific system or on a specific host species population can also provide access to an overall view of the functioning of the studied epidemiological system at a local scale. This review also emphasized the fact that very few studies addressed the bird density component when studying the role of birds in Lyme borreliosis *Borrelia* circulation while it can significantly affect their reservoir host potential. But host density is indeed intensively documented. We thus call for more interdisciplinary collaboration between epidemiology and ecology to reach an “OneHealth” approach of Lyme borreliosis dynamics in multi-host ecosystems.

Acknowledgment

We acknowledge the French Agency for Food, Environmental and Occupational Health & Safety (ANSES) and the DIM1HEALTH (Ile-de-France Regional Council) to support this work, and two anonymous reviewers for their helpful comments.

Conflict of interest

None

References

- Agoulon, A., Hoch, T., Heylen, D., Chalvet-Monfray, K., Plantard, O., 2019. Unravelling the phenology of *Ixodes frontalis*, a common but understudied tick species in Europe. *Ticks and tick-borne diseases* 10, 505-512.
- Anderson, J.F., 1988. Mammalian and avian reservoirs for *Borrelia burgdorferi*. *Annals of the New York Academy of Sciences* 539, 180-191.
- Anderson, J.F., 1989. Epizootiology of *Borrelia* in *Ixodes* tick vectors and reservoir hosts. *Reviews of infectious diseases* 11 Suppl 6, S1451-1459.
- Beckmann, S., Freund, R., Pehl, H., Rodgers, A., Venegas, T., 2019. Rodent species as possible reservoirs of *Borrelia burgdorferi* in a prairie ecosystem. *Ticks and tick-borne diseases* 10, 1162-1167.
- Bermúdez C, S.E., Torres, S., Aguirre, Y., Domínguez, L., Bernal Vega, J.A., 2015. A review of *Ixodes* (Acari: Ixodidae) parasitizing wild birds in Panama, with the first records of *Ixodes auritulus* and *Ixodes bequaerti*. *Systematic and Applied Acarology* 20, 847-853.
- Brinkerhoff, R.J., Folsom-O'Keefe, C.M., Tsao, K., Diuk-Wasser, M.A., 2011. Do birds affect Lyme disease risk? Range expansion of the vector-borne pathogen *Borrelia burgdorferi*. *Frontiers in Ecology and the Environment* 9, 103-110.
- Brisson, D., Dykhuizen, D.E., 2006. A modest model explains the distribution and abundance of *Borrelia burgdorferi* strains. *The American journal of tropical medicine and hygiene* 74, 615-622.
- Brunner, J.L., LoGiudice, K., Ostfeld, R.S., 2008. Estimating reservoir competence of *Borrelia burgdorferi* hosts: prevalence and infectivity, sensitivity, and specificity. *Journal of medical entomology* 45, 139-147.
- Castro, M.B., Wright, S.A., 2007. Vertebrate hosts of *Ixodes pacificus* (Acari: Ixodidae) in California. *Journal of vector ecology : journal of the Society for Vector Ecology* 32, 140-149.
- Comstedt, P., Jakobsson, T., Bergstrom, S., 2011. Global ecology and epidemiology of *Borrelia garinii* spirochetes. *Infection ecology & epidemiology* 1.
- De La Fuente, J., Estrada-Peña, A., Cabezas-Cruz, A., Brey, R., 2015. Flying ticks: Anciently evolved associations that constitute a risk of infectious disease spread. *Parasites and Vectors* 8.
- Dietrich, M., Gómez-Díaz, E., McCoy, K.D., 2011. Worldwide distribution and diversity of seabird ticks: Implications for the ecology and epidemiology of tick-borne pathogens. *Vector-Borne and Zoonotic Diseases* 11, 453-470.
- Dunn, J.M., Davis, S., Stacey, A., Diuk-Wasser, M.A., 2013. A simple model for the establishment of tick-borne pathogens of *Ixodes scapularis*: a global sensitivity analysis of R0. *Journal of theoretical biology* 335, 213-221.
- Estrada-Peña, A., Ostfeld, R.S., Peterson, A.T., Poulin, R., de la Fuente, J., 2014. Effects of environmental change on zoonotic disease risk: an ecological primer. *Trends in parasitology* 30, 205-214.
- Evans, D.E., Martins, J.R., Guglielmone, A.A., 2000. A review of the ticks (Acari, ixodida) of Brazil, their hosts and geographic distribution - 1. The state of Rio Grande do Sul, southern Brazil. *Memorias do Instituto Oswaldo Cruz* 95, 453-470.
- Falchi, A., Dantas-Torres, F., Lorusso, V., Malia, E., Lia, R.P., Otranto, D., 2012. Autochthonous and migratory birds as a dispersion source for *Ixodes ricinus* in southern Italy. *Exp. Appl. Acarol.* 58, 167-174.
- Gern, L., 2008. *Borrelia burgdorferi* sensu lato, the agent of lyme borreliosis: life in the wilds. *Parasite (Paris, France)* 15, 244-247.
- Gern, L., Estrada-Pena, A., Frandsen, F., Gray, J.S., Jaenson, T.G., Jongejan, F., Kahl, O., Korenberg, E., Mehl, R., Nuttall, P.A., 1998. European reservoir hosts of *Borrelia burgdorferi* sensu lato. *Zentralblatt fur Bakteriologie : international journal of medical microbiology* 287, 196-204.

- Giardina, A.R., Schmidt, K.A., Schaubert, E.M., Ostfeld, R.S., 2000. Modeling the role of songbirds and rodents in the ecology of Lyme disease. *Canadian journal of zoology* 78, 2184-2197.
- Gómez-Díaz, E., Boulinier, T., Sertour, N., Cornet, M., Ferquel, E., McCoy, K.D., 2011. Genetic structure of marine *Borrelia garinii* and population admixture with the terrestrial cycle of Lyme borreliosis. *Environmental microbiology* 13, 2453-2467.
- Gonzalez-Acuna, D., Venzal, J.M., Keirans, J.E., Robbins, R.G., Ippi, S., Guglielmone, A.A., 2005. New host and locality records for the *Ixodes auritulus* (Acari: Ixodidae) species group, with a review of host relationships and distribution in the Neotropical Zoogeographic Region. *Experimental & applied acarology* 37, 147-156.
- Hartemink, N., Randolph, S., Davis, S., Heesterbeek, J., 2008. The basic reproduction number for complex disease systems: Defining R_0 for tick-borne infections. *The American Naturalist* 171, 743-754.
- Hasle, G., 2013. Transport of ixodid ticks and tick-borne pathogens by migratory birds. *Frontiers in cellular and infection microbiology* 3, 48.
- Heffernan, J.M., Lou, Y., Wu, J., 2014. Range expansion of *Ixodes scapularis* ticks and of *Borrelia burgdorferi* by migratory birds. *Discrete and Continuous Dynamical Systems - Series B* 19, 3147-3167.
- Heylen, D., Adriaensen, F., Van Dongen, S., Sprong, H., Matthysen, E., 2013. Ecological factors that determine *Ixodes ricinus* tick burdens in the great tit (*Parus major*), an avian reservoir of *Borrelia burgdorferi* s.l. *International journal for parasitology* 43, 603-611.
- Heylen, D., De Coninck, E., Jansen, F., Madder, M., 2014. Differential diagnosis of three common *Ixodes* spp. ticks infesting songbirds of Western Europe: *Ixodes arboricola*, *I. frontalis* and *I. ricinus*. *Ticks and tick-borne diseases* 5, 693-700.
- Heylen, D., Krawczyk, A., Lopes de Carvalho, I., Nuncio, M.S., Sprong, H., Norte, A.C., 2017. Bridging of cryptic *Borrelia* cycles in European songbirds. *Environmental microbiology* 19, 1857-1867.
- Heylen, D., Lasters, R., Adriaensen, F., Fonville, M., Sprong, H., Matthysen, E., 2019. Ticks and tick-borne diseases in the city: Role of landscape connectivity and green space characteristics in a metropolitan area. *Science of the total environment* 670, 941-949.
- Hofmeester, T.R., Coipan, E.C., Van Wieren, S.E., Prins, H.H.T., Takken, W., Sprong, H., 2016. Few vertebrate species dominate the *Borrelia burgdorferi* s.l. life cycle. *Environmental Research Letters* 11.
- Huang, C.-I., Kay, S.C., Davis, S., Tufts, D.M., Gaffett, K., Tefft, B., Diuk-Wasser, M.A., 2019. High burdens of *Ixodes scapularis* larval ticks on white-tailed deer may limit Lyme disease risk in a low biodiversity setting. *Ticks and tick-borne diseases* 10, 258-268.
- Hubalek, Z., 2004. An annotated checklist of pathogenic microorganisms associated with migratory birds. *Journal of wildlife diseases* 40, 639-659.
- Humair, P.F., 2002. Birds and *Borrelia*. *International journal of medical microbiology : IJMM* 291 Suppl 33, 70-74.
- Humair, P.F., Postic, D., Wallich, R., Gern, L., 1998. An avian reservoir (*Turdus merula*) of the Lyme borreliosis spirochetes. *Zentralblatt für Bakteriologie : international journal of medical microbiology* 287, 521-538.
- Jaenson, T.G., Talleklint, L., Lundqvist, L., Olsen, B., Chirico, J., Mejlön, H., 1994. Geographical distribution, host associations, and vector roles of ticks (Acari: Ixodidae, Argasidae) in Sweden. *Journal of medical entomology* 31, 240-256.
- Jiguet, F., Devictor, V., Julliard, R., Couvet, D., 2012. French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. *Acta Oecologica* 44, 58-66.
- Jones, K.E., Patel, N.G., Levy, M.A., Storeygard, A., Balk, D., Gittleman, J.L., Daszak, P., 2008. Global trends in emerging infectious diseases. *Nature* 451, 990-993.
- Jongejan, F., Uilenberg, G., 2004. The global importance of ticks. *Parasitology* 129, S3-S14.

- Karbowiak, G., Biernat, B., Stanczak, J., Werszko, J., Szewczyk, T., Sytykiewicz, H., 2018. The role of particular ticks developmental stages in the circulation of tick-borne pathogens in Central Europe. 5. *Borreliaceae*. *Annals of parasitology* 64, 151-171.
- Keesing, F., Brunner, J., Duerr, S., Killilea, M., Logiudice, K., Schmidt, K., Vuong, H., Ostfeld, R.S., 2009. Hosts as ecological traps for the vector of Lyme disease. *Proceedings. Biological sciences* 276, 3911-3919.
- Klitgaard, K., Højgaard, J., Isbrand, A., Madsen, J.J., Thorup, K., Bødker, R., 2019. Screening for multiple tick-borne pathogens in *Ixodes ricinus* ticks from birds in Denmark during spring and autumn migration seasons. *Ticks Tick Borne Dis* 10, 546-552.
- Kolonin, G.V., 2008. Birds as hosts of ixodid ticks (Acarina, Ixodidae). *Entomological Review* 88, 1012-1015.
- Kurtenbach, K., Hanincová, K., Tsao, J.I., Margos, G., Fish, D., Ogden, N.H., 2006. Fundamental processes in the evolutionary ecology of Lyme borreliosis. *Nature Reviews Microbiology* 4, 660-669.
- Levi, T., Keesing, F., Holt, R.D., Barfield, M., Ostfeld, R.S., 2016. Quantifying dilution and amplification in a community of hosts for tick-borne pathogens. *Ecological applications : a publication of the Ecological Society of America* 26, 484-498.
- Levrel, H., Fontaine, B., Henry, P.-Y., Jiguet, F., Julliard, R., Kerbiriou, C., Couvet, D., 2010. Balancing state and volunteer investment in biodiversity monitoring for the implementation of CBD indicators: A French example. *Ecological economics* 69, 1580-1586.
- Liberati, A., Altman, D.G., Tetzlaff, J., Mulrow, C., Gøtzsche, P.C., Ioannidis, J.P., Clarke, M., Devereaux, P.J., Kleijnen, J., Moher, D., 2009. The PRISMA statement for reporting systematic reviews and meta-analyses of studies that evaluate health care interventions: explanation and elaboration. *Journal of clinical epidemiology* 62, e1-e34.
- LoGiudice, K., Ostfeld, R.S., Schmidt, K.A., Keesing, F., 2003. The ecology of infectious disease: effects of host diversity and community composition on Lyme disease risk. *Proceedings of the National Academy of Sciences of the United States of America* 100, 567-571.
- Loss, S.R., Noden, B.H., Hamer, G.L., Hamer, S.A., 2016. A quantitative synthesis of the role of birds in carrying ticks and tick-borne pathogens in North America. *Oecologia* 182, 947-959.
- Magnarelli, L.A., 2011. The Role of Vertebrate Hosts in Tick-Borne Infections. *Clinical Microbiology Newsletter* 33, 17-20.
- Marsot, M., Henry, P.Y., Vourc'h, G., Gasqui, P., Ferquel, E., Laignel, J., Grysan, M., Chapuis, J.L., 2012. Which forest bird species are the main hosts of the tick, *Ixodes ricinus*, the vector of *Borrelia burgdorferi* sensu lato, during the breeding season? *International journal for parasitology* 42, 781-788.
- Martello, E., Mannelli, A., Grego, E., Ceballos, L.A., Ragagli, C., Stella, M.C., Tomassone, L., 2019. *Borrelia burgdorferi* sensu lato and spotted fever group rickettsiae in small rodents and attached ticks in the Northern Apennines, Italy. *Ticks and tick-borne diseases* 10, 862-867.
- McCoy, K.D., Boulanger, N., 2015. Tiques et maladies à tiques: biologie, écologie évolutive, épidémiologie.
- Mysterud, A., Heylen, D.J.A., Matthysen, E., Garcia, A.L., Jore, S., Viljugrein, H., 2019a. Lyme neuroborreliosis and bird populations in northern Europe. *Proc. Biol. Sci.* 286, 20190759.
- Mysterud, A., Heylen, D.J.A., Matthysen, E., Garcia, A.L., Jore, S., Viljugrein, H., 2019b. Lyme neuroborreliosis and bird populations in northern Europe. *Proceedings. Biological sciences* 286, 20190759.
- Mysterud, A., Stigum, V.M., Linlokken, H., Herland, A., Viljugrein, H., 2019c. How general are generalist parasites? The small mammal part of the Lyme disease transmission cycle in two ecosystems in northern Europe. *Oecologia* 190, 115-126.

- 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. *Environmental microbiology* 15, 386-397.
- Oliver Jr, J.H., 1989. Biology and systematics of ticks (Acari: Ixodida). *Annual review of Ecology and Systematics* 20, 397-430.
- Ostfeld, R.S., Levi, T., Jolles, A.E., Martin, L.B., Hosseini, P.R., Keesing, F., 2014. Life history and demographic drivers of reservoir competence for three tick-borne zoonotic pathogens. *PLoS one* 9, e107387.
- Pisanu, B., Marsot, M., Marmet, J., Chapuis, J.L., Reale, D., Vourc'h, G., 2010. Introduced Siberian chipmunks are more heavily infested by ixodid ticks than are native bank voles in a suburban forest in France. *International journal for parasitology* 40, 1277-1283.
- Randolph, S., 1998. Ticks are not insects: consequences of contrasting vector biology for transmission potential. *Parasitology Today* 14, 186-192.
- Randolph, S.E., Craine, N.G., 1995. General framework for comparative quantitative studies on transmission of tick-borne diseases using Lyme borreliosis in Europe as an example. *Journal of medical entomology* 32, 765-777.
- Reed, K.D., Meece, J.K., Henkel, J.S., Shukla, S.K., 2003. Birds, migration and emerging zoonoses: west nile virus, lyme disease, influenza A and enteropathogens. *Clinical medicine & research* 1, 5-12.
- Richter, D., Debski, A., Hubalek, Z., Matuschka, F.-R., 2012. Absence of Lyme disease spirochetes in larval *Ixodes ricinus* ticks. *Vector-Borne and Zoonotic Diseases* 12, 21-27.
- Sala, V., De Faveri, E., 2016. Epidemiology of lyme disease in domestic and wild animals. *Open Dermatology Journal* 10, 15-26.
- Schmeller, D., Henle, K., Loyau, A., Besnard, A., Henry, P.-Y., 2012. Bird-monitoring in Europe—a first overview of practices, motivations and aims. *Nature Conservation* 2, 41.
- Sonenshine, D.E., Roe, R.M., 2013. *Biology of ticks*. Oxford University Press.
- Sparagano, O., George, D., Giangaspero, A., Špitalská, E., 2015. Arthropods and associated arthropod-borne diseases transmitted by migrating birds. The case of ticks and tick-borne pathogens. *Veterinary parasitology* 213, 61-66.
- Stafford, K.C., 3rd, Bladen, V.C., Magnarelli, L.A., 1995. Ticks (Acari: Ixodidae) infesting wild birds (Aves) and white-footed mice in Lyme, CT. *Journal of medical entomology* 32, 453-466.
- Stanek, G., Wormser, G.P., Gray, J., Strle, F., 2012. Lyme borreliosis. *The Lancet* 379, 461-473.
- Tamzali, Y., 2013. Equine piroplasmiasis: An updated review. *Equine Veterinary Education* 25, 590-598.
- Toledo, Á., Olmeda, A.S., Escudero, R., Jado, I., Valcárcel, F., Casado-Nistal, M.A., Rodríguez-Vargas, M., Gil, H., Anda, P., 2009. Tick-borne zoonotic bacteria in ticks collected from central Spain. *The American journal of tropical medicine and hygiene* 81, 67-74.
- van Duijvendijk, G., Sprong, H., Takken, W., 2015. Multi-trophic interactions driving the transmission cycle of *Borrelia afzelii* between *Ixodes ricinus* and rodents: a review. *Parasites & vectors* 8, 643.
- Wu, X., Rost, G., Zou, X., 2016. Impact of spring bird migration on the range expansion of *Ixodes scapularis* tick population. *Bulletin of mathematical biology* 78, 138-168.

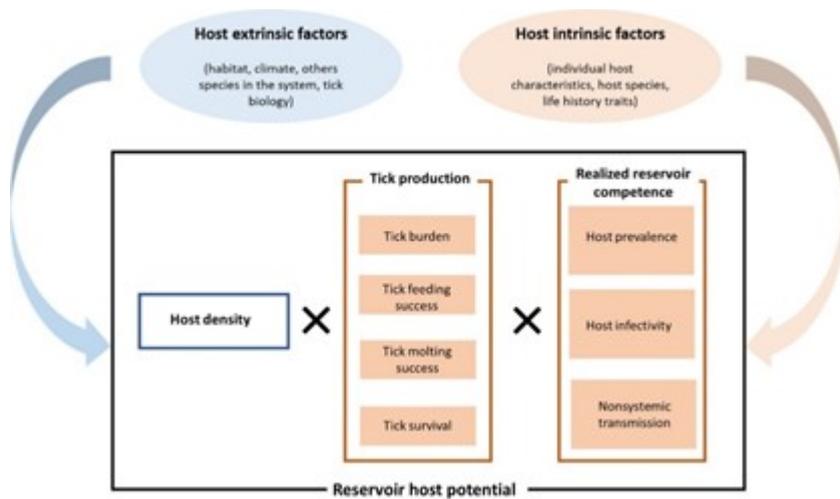


Figure 1: Overview diagram of the parameters that determine the reservoir host potential and different factors that may influence them in the context of a tick-borne disease (inspired of Brunner, LoGiudice, and Ostfeld 2008). Bold boxes represent the components related to the host (orange) and to the environment (blue) that determine the reservoir host potential of a given host species population. Colorfull boxes represent the different parameters that define these components and circles represent the host intrinsic (orange) and extrinsic (blue) factors that could influence the parameters.

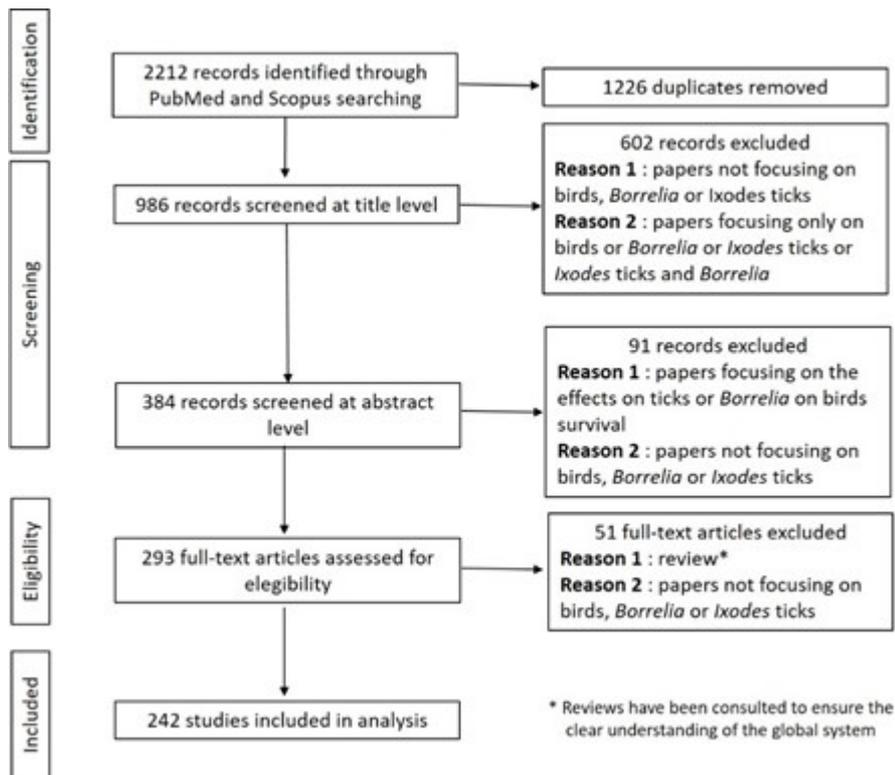


Figure 2: PRISMA flow diagram of the selection process

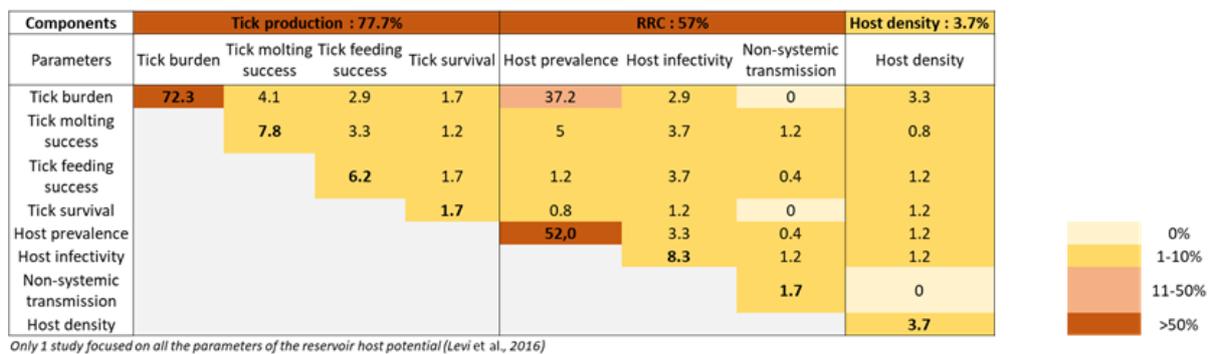
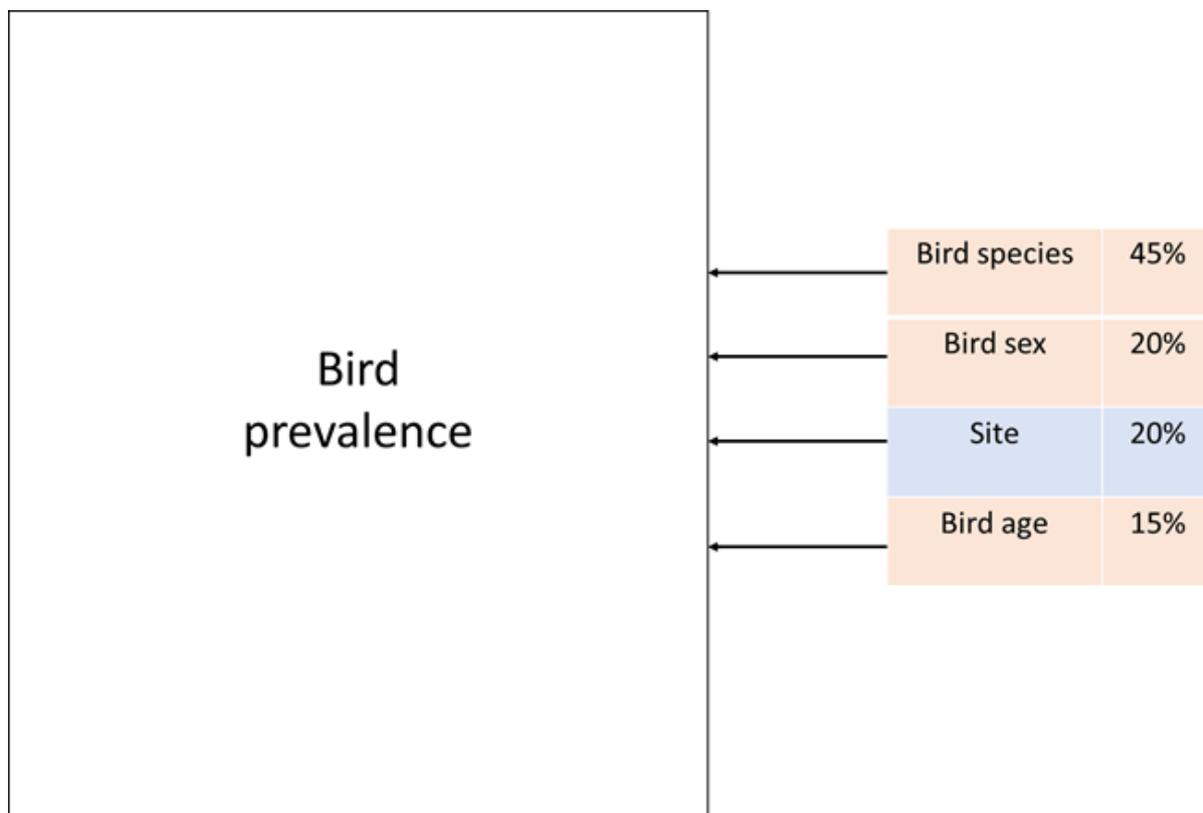
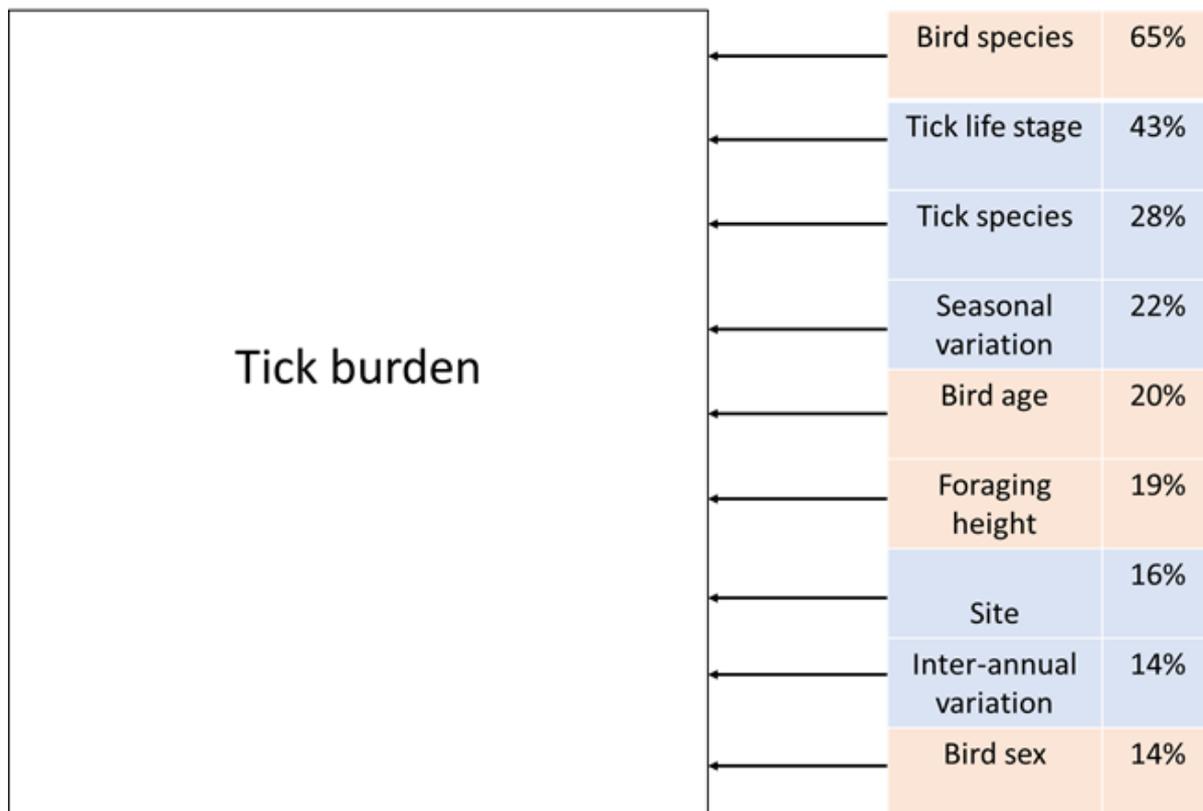


Figure 3: Percent of studies worldwide focusing on the reservoir host potential (RHP) of wild birds for Lyme borreliosis *Borrelia* circulation ($n_{tot}=242$) according to the RHP components, parameters and combination of parameters.



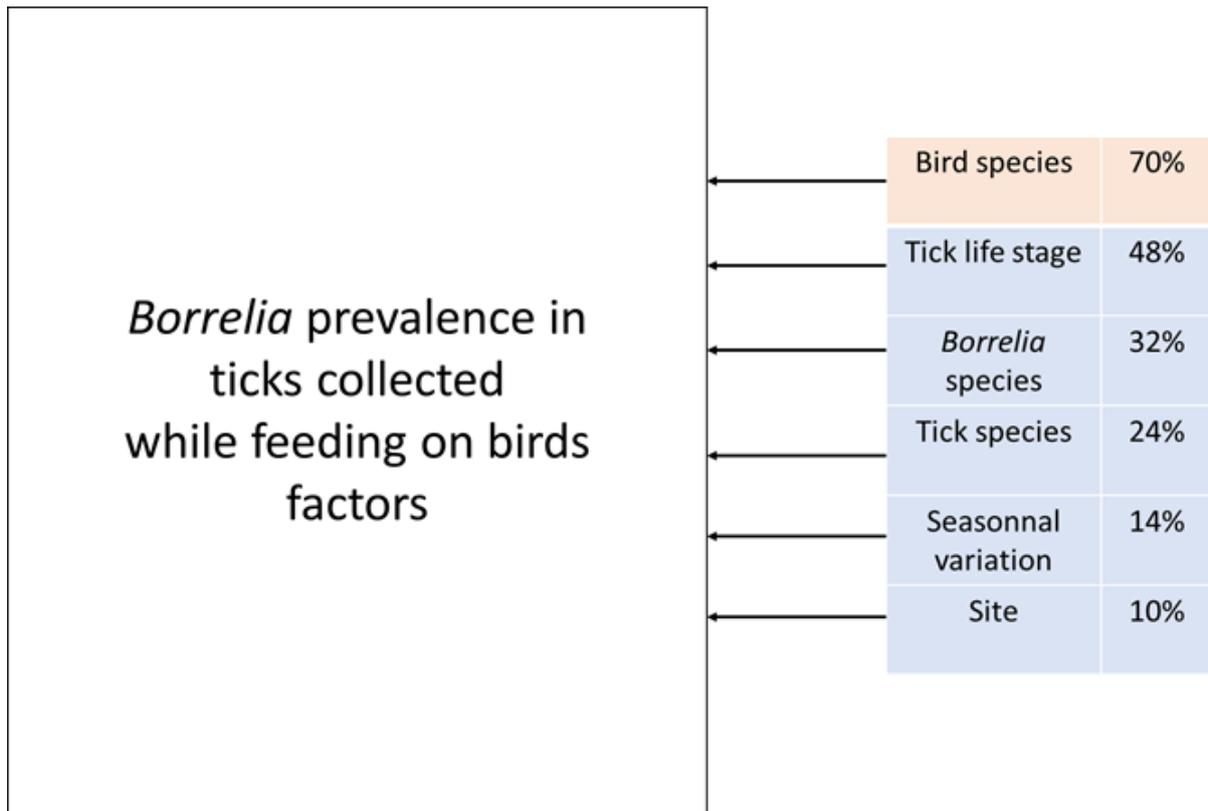


Figure 4: Percent of European studies ($n_{\text{tot}}=118$) focusing on the reservoir host potential (RHP) of wild birds for Lyme borreliosis *Borrelia* circulation according to the major host intrinsic (light red) and extrinsic (blue) factors influencing the bird tick burden ($n_{\text{tot}}=74$), the *Borrelia* prevalence in birds ($n_{\text{tot}}=20$) and the *Borrelia* prevalence in ticks collected while feeding on birds ($n_{\text{tot}}=50$).

Table 1: Definitions of the different components (bold) and parameters that define the reservoir host potential (RHP) of a given host species population in a tick-borne disease.

RHP components and parameters	Definitions
Tick production	Number of ticks produced by a host species population
Tick burden	Number of ticks fed by a host species population. It can be influenced by host-intrinsic factors (species, individual characteristics, life-history traits) and host-extrinsic factors (habitat, weather conditions, and tick biology).
Tick feeding success	Probability that ticks feed successfully. It depends on tick attachment success and blood meal success. It can be influenced by host-intrinsic factors (species, individual characteristics, life-history traits) and host-extrinsic factors (habitat, weather conditions, and tick biology).
Tick moulting success	Probability that ticks successfully moult after a blood meal. It can be influenced by host-intrinsic factors (species, individual characteristics, life-history traits) and host-extrinsic factors (habitat, weather conditions, and tick biology).
Tick survival	Probability that ticks survive while they are attached on the host, and once they are free in the environment. It can be influenced by host-intrinsic factors (species, individual characteristics, life-history traits) and host extrinsic factors (habitat, weather conditions, and tick biology).
Realized reservoir competence	Host species population ability to infect ticks
Host prevalence	Probability that the host is infected. It can be influenced by host-intrinsic factors (species, individual characteristics, life-history traits) and host-extrinsic factors (habitat, weather conditions, and tick biology).
Host infectivity	Probability that the infected host transmits the pathogen to the tick. It can be influenced by host-intrinsic factors (species, individual characteristics, life history traits) and host-extrinsic factors (habitat, weather conditions, and tick biology).
Non-systemic transmission	Transmission of the infection between ticks feeding closely on the host (co-feeding). It does not necessarily imply host infection. It can be influenced by host-intrinsic factors (species, individual characteristics, life history traits) and host-extrinsic factors (habitat, weather

conditions, and tick biology).

Host density

Number of individuals in a given host species population
