



## Which forest bird species are the main hosts of the tick, *Ixodes ricinus*, the vector of *Borrelia burgdorferi* sensu lato, during the breeding season?

M. Marsot<sup>a,b,1</sup>, P.-Y. Henry<sup>c,1</sup>, G. Vourc'h<sup>a,\*</sup>, P. Gasqui<sup>a</sup>, E. Ferquel<sup>d</sup>, J. Laignel<sup>b</sup>, M. Grysan<sup>b</sup>, J.-L. Chapuis<sup>b</sup>

<sup>a</sup> INRA, UR346, Epidémiologie Animale, F-63122 Saint Genès Champanelle, France

<sup>b</sup> MNHN, Département Ecologie et Gestion de la Biodiversité, UMR 7204 MNHN-CNRS-PG, 61 Rue Buffon, CP 53, F-75005 Paris, France

<sup>c</sup> MNHN, Département Ecologie et Gestion de la Biodiversité, UMR 7179 MNHN-CNRS, 1 Avenue du Petit Château, F-91800 Brunoy, France

<sup>d</sup> Institut Pasteur, Centre National de Référence des *Borrelia*, 25–28 Rue du Docteur Roux, F-75724 Paris Cedex 15, France

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### ABSTRACT

Wild birds are important hosts for vector-borne pathogens, especially those borne by ticks. However, few studies have been conducted on the role of different bird species within a community as hosts of vector-borne pathogens. This study addressed individual and species factors that could explain the burden of *Ixodes ricinus* on forest birds during the reproductive periods of both vectors and hosts. The goal was to identify which bird species contribute the most to the tick population at the community level. Birds were mist-netted on four plots in 2008 and on seven plots in 2009 in two forests (Sénart and Notre Dame, near Paris, France). The dependence of the tick load per bird upon environmental conditions (questing nymph density, year and plot) and on host species traits (species, age, sex, body size, vertical space use, level of innate and acquired immunity) was analysed. Finally, the relative contribution of each bird species to the local dynamics of ticks was estimated, while accounting for their respective abundance. Tick burden differed markedly between bird species and varied according to questing nymph density. Bird species with a high body mass, those that forage low in the vegetation, and those that had a high innate immune response and a high spleen mass were more likely to have a high tick burden. Four species (the Common Blackbird, *Turdus merula*, the European Robin, *Erithacus rubecula*, the Song Thrush, *Turdus philomelos*, and the Winter Wren, *Troglodytes troglodytes*) hosted more than 90% of the ticks in the local bird community. These species, and particularly *T. merula* which was host to a high proportion of the nymphs, are likely to contribute significantly to the circulation of pathogens for which they are competent, such as the agent of Lyme borreliosis.

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### 1. Introduction

The increasing emergence of zoonotic vector-borne diseases over the last 15 years has drawn attention to their complex ecology (Jones et al., 2008). In particular, it has highlighted the necessity to better evaluate the rate of contact between vectors, reservoir hosts and humans (Jones et al., 2008). Wild birds are important hosts for vector-borne pathogens in North America and Eurasia, especially those borne by ticks (Ogden et al., 2008). However, the role of bird species in the local dynamics of tick-borne pathogens during their reproductive seasons has been poorly studied (but see Battaly et al., 1987; Battaly and Fish, 1993; Hamer et al., 2011; James et al., 2011).

The majority of studies on bird-borne ticks has focused on the role of migrating birds in disseminating tick-transmitted pathogens over long distances, and consequently has examined tick burdens during bird migrations (Olsen et al., 1995; Comstedt et al., 2006; Ogden et al., 2008; Dubska et al., 2009). Avian mobility and migration are epizootiologic factors that potentially increase the dissemination of vector-borne pathogens (Hubalek, 2004; Ogden et al., 2008; Brinkerhoff et al., 2011). However, in addition to disseminating ticks – and tick-borne pathogens – over long distances during migration periods, birds may also play a major role in the dynamics of local tick populations and associated pathogens during the reproductive periods of both birds and ticks. Most larvae and nymphs are found between May and June (Gray, 2002), i.e. the same time that birds are sedentary and settled in their reproductive territories.

Epidemiological research on rodents has shown that the tick burden is influenced by three main variables: the density of questing ticks on vegetation (Dorn et al., 1999; Schmidt et al.,

\* Corresponding author. Tel.: +33 473 62 47 26; fax: +33 473 62 45 48.

E-mail address: [gvourc@clermont.inra.fr](mailto:gvourc@clermont.inra.fr) (G. Vourc'h).

<sup>1</sup> These authors contributed equally to the work.

1999; Randolph, 2004), and the age and sex of individual hosts (Tälleklint and Jaenson, 1997; Dorn et al., 1999). Tick burden also varies among species (Kurtenbach et al., 1995). This inter-specific variation is explained by: differences in body size (Harrison et al., 2010) – bigger host species have more ticks; differences in immunocompetency (Hughes and Randolph, 2001) – some species defend themselves against ticks better than others; and space use (Boyer et al., 2010) – the larger their home range, the more likely they are to encounter ticks.

In this study, we analysed individual and species variables which could explain the tick burden on territorial, reproductive birds and we estimated which species contribute most to the tick population. Extending the findings on rodents to birds, the following set of predictions was formulated. First, bird tick burdens would be determined largely by questing nymph density (Dorn et al., 1999; Schmidt et al., 1999). Second, tick burdens would be higher in adults than in juveniles, given that nestlings are free of ticks (Gregoire et al., 2002) and that the colonization of young hosts takes time (although this time lag is not known). Third, during the reproductive period, female passerines spend more time incubating the eggs and less time patrolling the territory than males. Therefore, active males were predicted to bear more ticks than females during the reproductive period. At the community level, species are not likely to be equally infested. A set of variables most likely modulates the probability that a species bears ticks. Our fourth prediction therefore was that larger species would be more likely to host a greater number of ticks than small species because they expose larger areas of skin suitable for tick attachment and cope better with parasitism than smaller individuals. Fifth, since questing ticks do not climb higher than 1.5 m (Meljon and Jaenson, 1997), species spending much of their active period close to the ground would be more heavily infested by ticks than others. Breeding birds are expected to be particularly exposed to ticks during two main activities: when foraging and/or when accessing their nest to care for their chicks. Therefore the effects of average foraging height and of average nest height on tick burden were tested separately: the use of lower strata was predicted to be associated with a higher tick burden. Moreover, hosts defend themselves against tick infestation by launching immune responses when a tick tries to feed. The innate immunity, and particularly the local inflammatory response, probably helps to deter ticks (Prosdocimi et al., 2010). Acquired immunity is also known to contribute to protection against tick infestation (Trager, 1939; Akhtar et al., 2011). The sixth prediction therefore was that, since allocation of resources to immune defences varies among species (Møller and Erritzoe, 2002), the more a species allocates to innate and/or acquired immunity, the lower would be its tick burden. The size of the skin swelling elicited by the injection of mitogen phytohemagglutinin (referred to hereafter as the PHA response) was interpreted as an indicator of the strength of the inflammatory response (Martin et al., 2006), the first major component of the innate immune response. Furthermore, the mass of the spleen was used as an index of the investment in the acquired immune response at the species level (Møller et al., 2000; Møller and Erritzoe, 2002). The tick burden was predicted to be negatively related to PHA values and to spleen mass.

Lyme borreliosis is the most prevalent vector-borne disease affecting humans in temperate zones of the northern hemisphere (Smith et al., 2006; Bacon et al., 2008; Rizzoli et al., 2011). In Europe, it is transmitted by *Ixodes ricinus*. This tick species is a generalist parasite which goes through three active developmental stages (larval, nymph and adult). During each stage, with the exception of adult males, the tick takes one blood meal on a vertebrate host either to moult (larvae, nymphs) or to reproduce (Gern, 2008). Lyme borreliosis is caused by pathogenic bacteria belonging

to the genospecies complex of *Borrelia burgdorferi* sensu lato (sl), mostly *Borrelia burgdorferi* sensu stricto (ss), *Borrelia afzelii*, *Borrelia bavariensis*, *Borrelia garinii*, *Borrelia spielmanii* and *Borrelia valaisiana* (van Dam et al., 1993; Stanek and Reiter, 2011). Reservoir hosts which maintain *B. burgdorferi* sl are normally infected by nymphs and transmit it to uninfected larvae (Gern and Humair, 2002). The role of rodents as reservoir hosts is crucial for some *Borrelia* spp. such as *B. afzelii*, *B. bavariensis* (in Europe) and *B. burgdorferi* ss (in the USA and to a lesser extent in Europe) (Mather et al., 1989; Humair et al., 1995; Peavey et al., 1997; Humair and Gern, 1998; Hanincová et al., 2003a), but birds are also important in maintaining certain genospecies such as *B. garinii* and *B. valaisiana* in Europe (Humair et al., 1998; Kurtenbach et al., 1998; Hanincová et al., 2003b) and *B. burgdorferi* ss in the USA (Brinkerhoff et al., 2011; Hamer et al., 2011).

Understanding the contribution of alternative reservoirs to rodents such as birds in an enzootic area for *B. burgdorferi* sl is a prerequisite for advancing prevention strategies for Lyme borreliosis (Tsao et al., 2004; Hamer et al., 2011). This is particularly true in areas where host habitats overlap with those of humans. Because infected nymphs are the source of infection to reservoir hosts, we also tested whether the proportion of nymphs differed between species. Species bearing more nymphs than average would contribute the most to the dynamics of *B. burgdorferi* sl. Then, the relative contribution of each bird species to the local dynamics of tick populations was evaluated using an “index of importance” for each bird species, corresponding to the product of the estimated mean tick burden and the relative abundance of the bird species (from James et al., 2011, but we corrected for between-species variation in capturability). For a given bird species in a community, a high tick burden or a high abundance of the host were assumed to be of equal importance in determining the contribution of the species to the local tick dynamics. This index of importance was also stratified to reflect the stage distribution of ticks (nymphs versus larvae) on each host species. These parameters characterizing the host-parasite association were assessed, in 2008–2009, on a community of breeding forest birds in northern France, where *I. ricinus* is the main vector of Lyme borreliosis.

## 2. Materials and methods

### 2.1. Study sites

The study was conducted 22 km southeast of Paris (France) at two sites, Sénart forest (3200 hectares (ha), 02°29'E, 48°40'N, 80 m above sea level) and Notre Dame forest (2200 ha, 02°35'E, 48°45'N, 100 m), both oak-hornbeam forests. The study plots were essentially composed of broad-leaved trees dominated by oaks (*Quercus robur*, *Quercus pedunculata*) and European hornbeams (*Carpinus betulus*), with two other forest tree species, the sweet chestnut (*Castanea sativa*) and the lime tree (*Tilia vulgaris*) in certain areas (Marmet, 2008).

The avian community is composed of common forest birds, and is dominated by passerines (Laury, 2007). Birds were mist-netted on four plots in the Sénart forest in 2008, and on five plots (including those of 2008) in the Sénart forest and two plots in the Notre Dame forest in 2009. The plots were chosen so that they were representative of the average forest cover. A plot was a 4 ha square of 16 vertical mist-nets (12 m long and 2.5 m high) located 50 m from each other. Mist-nets intercepted birds between 0.4 and 2.9 m from the ground. Bird sampling was conducted during the peak of activity of questing ticks, namely between June and July 2008 and between May and June 2009, with a frequency of one morning capture session per week per plot over 4 weeks.

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