



Impacts of deer management practices on the spatial dynamics of the tick *Ixodes ricinus*: A scenario analysis



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ABSTRACT

Deer, for example roe deer, red deer and fallow deer, are the common reproduction host types for European *Ixodes ricinus* ticks. Understanding the consequences of deer management on the spatial dynamics of ticks may advise the risk management of tick-borne diseases, and thus be of public health importance. We present a scenario analysis to understand such consequences by integrating multi-disciplinary knowledge within a predictive modelling framework. A spatial tick population model was adopted to explore how changes in the host population may affect woodland patch- and landscape-level tick dynamics. Scenarios on current and foreseen European deer management strategies were built based on expert knowledge. These scenarios were then tested through the described model for their potential effectiveness as tick control strategies. Our models indicate that: (i) reducing local deer densities could not effectively reduce tick abundance if woodland patches are well-connected, allowing deer population exchanges, (ii) controlling deer grazing intensity in grassland may not be an effective tick control strategy, (iii) local extinction of deer could decrease tick abundance considerably but deer reintroduction could lead to fast tick upsurge, and (iv) controlling human disturbances may reduce the tick density at landscape-level, as well as tick “hotspots” (i.e., areas with unusually high tick density) at woodland patch-level. Our results can instruct policy-makers on the potential impact on public health of wildlife management strategies, and suggest empirical investigations of disease risks. For optimising such simulation studies on disease risks, however, a better understanding of how biodiversity may influence the ecology of tick and pathogen transmission is required.

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1. Introduction

Ixodes ricinus (Acari: Ixodidae) is the most abundant and widely distributed tick species in Europe. Over the past two decades, the reported incidence of tick-borne diseases, such as Lyme borreliosis and tick-borne encephalitis, has increased in Europe (Randolph, 2008). This has made tick-borne zoonoses the most prevalent vector-borne diseases in Europe and hence kindled public health and scientific attention (Morens et al., 2004).

Host availability is fundamental for the maintenance of ticks and pathogen populations (Ruiz-Fons and Gilbert, 2010). Success

in managing tick-borne diseases depends on understanding tick dynamics, including the way in which tick feeding success is affected by varying host population densities and distributions. *Ixodes* ticks feed on a broad range of hosts. *I. ricinus* larvae primarily feed on small-sized animals such as rodents and insectivores (Gray et al., 1994; Jaenson and Talleklint, 1996), while hosts for nymphs are less specific, including birds, and small, medium, and large-sized mammals (Estrada-Peña et al., 2005). Adult ticks often have a narrower host range, with medium- and large-sized hosts, for example deer (Rizzoli et al., 2009; Tagliapietra et al., 2011). This three-host tick life cycle can be impacted by a diapause occurring at different life stages such that its duration may extend over two years (Gray, 1981). *Ixodes* ticks can be transported across the landscape as hosts move. Landscape effects, e.g., woodland fragmentation, shaping host distribution and limiting host movement at different spatial scales, can yield different influences on tick populations in different life stages (Li et al., 2012a). Deer and other large mammals are the target of direct management practices (e.g., fencing, hunting, translocation, etc.). In previous empirical studies,

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deer density has been found to be positively related to tick densities and the tick infestations on rodents (Cagnacci et al., 2012; Killilea et al., 2008). There is a need to analyse the potential consequences of these management practices on the spatial dynamics of ticks, so that both wildlife managers and the public would be better informed about potential changes in disease risks (Luckhart et al., 2010).

Predicting the impact of deer management on the spatial dynamics of *I. ricinus* requires a thorough understanding of (i) deer management practices, (ii) the spatially explicit response of deer movement patterns to such management practices and (iii) the spatial ecology of tick-deer relations. Agent-based modelling and cellular automata have the capacity to integrate these aspects (Grimm et al., 2005). To date, only a few studies have reported on biological process-based models modelling tick populations in a spatially explicit way (Killilea et al., 2008). These models have been used mainly to explore how spatial dynamics of tick densities and/or infections can be influenced by landscape heterogeneity and host movements. Some recent examples are: a multi-habitat model (Hoch et al., 2010) for *I. ricinus* tick, an agent-based model (Wang et al., 2012) for *Amblyomma americanum*, a multi-patch model (Watts et al., 2009) and a reaction diffusion model (Jones et al., 2011) for louping-ill virus, and a cellular automata model for Lyme disease (Li et al., 2012a). In general, these studies support either a single host following a random exploratory movement or assume a certain number of hosts continuously travelling between woodland patches. However, in the field, animals can exhibit a set of statistically distinguishable movement patterns as a function of their internal state, motion capacity, navigation capacity, environmental conditions and the management strategies impacting them (Nathan et al., 2008). Therefore, a multiphasic hypothesis for the host movement pattern (i.e., considering more than one host movement phase, e.g., both home-ranging phase, in which animals randomly move within their home range, and displacement phase, in which animals tend to move over longer distances for new habitats) may be an interesting extension to the current spatial tick modelling context.

This study aimed to investigate the consequences of deer management practices on the spatial dynamics of ticks. We firstly described a spatial tick model adapted from a previous study (Li et al., 2012a). Then, based on expert knowledge, four scenarios of current and foreseen deer management practices were built, namely: (i) reducing local deer density, (ii) controlling deer grazing intensity in grassland, (iii) translocation of deer species, and (iv) controlling human disturbance and deer displacement between woodland patches. The influence on the spatial dynamics of ticks under these scenarios was tested through the model. Finally, we discussed these results with a focus on the effectiveness of these practices as tick controlling strategies.

2. Materials and methods

2.1. Model profile

The cellular automata model for the spatial ecology of ticks was adapted from Li et al. (2012a) and included significant modifications compared to the original model. Firstly, the tick feeding pattern was more detailed to better represent the reality by enabling low probabilities for adults to feed on small mammals (Cagnacci et al., 2012) and larvae to feed on deer (Kiffner et al., 2010). The simplified method based on fixed tick attachment rates in the original model was replaced by a more detailed one based on host-finding probabilities of ticks and controlled by the feeding capacities of ticks on hosts. This adaption further allows to simulate the effects of deer density, as a tick amplifier, on tick infestation

levels (Cagnacci et al., 2012). Secondly, rules for deer movement were developed to distinguish behaviours in home-ranging and displacement phases, allowing to represent more realistic deer movement patterns. Finally, pathogen transmission functions were not included as the study at hand focused on tick populations. The modifications aimed at improving the model's specificity, as the focus in this study was on the effects of the movements of the major host types on the abundance and distribution of ticks.

The model was coded into Repast Symphony (North et al., 2006). The space used was two-dimensional and organised as a lattice of cells. Each cell in the lattice had three layers: a tick population, a host population and a landscape layer. The lattice was programmed to evolve in discrete time steps following a set of transition rules to update the cell states simultaneously. The present model adopts a cell size of 1 ha and a time step of 1 week.

2.1.1. States and parameters

The three layers of cell states were:

Tick population layer: A “larva”–“nymph”–“adult” life stage structure was used (Fig. 1). In each stage, ticks could be in questing, feeding or interstadial development phases. When encountering hosts, questing ticks attached for blood meals, then dropped and developed into the next life stages. Female adult ticks (assuming half of the emerged adult ticks were females) also needed blood meals to produce (i.e., lay eggs that hatch into) larval ticks.

Host population layer: Two generalised host types were used: small mammals (including rodents and lagomorphs) and deer. Each life stage of the ticks was assumed capable of feeding on both host types. The overall number of the two host types was fixed but the host distributions could vary between time steps as a result of movements. Indeed, host movements resulted in ticks being transported from one place to another.

Landscape layer: The cell states used were “woodland”–“grassland”–“non-vegetated areas”. Deer were considered to inhabit woodland mostly and to spend a proportion of time in grassland. Ticks could inhabit grassland but woodland was considered more suitable. Small mammals could inhabit both woodland and grassland. Mortality rates of ticks, densities of hosts and movement patterns of hosts varied with land cover types. Hosts could enter non-vegetated areas, but would not stay, meaning that no ticks would drop off in non-vegetated area. The landscape layer was set static and could be based on either real or theoretical landscape maps.

Parameters in the model were estimated from field and laboratory observations found in the literature (Table 1).

2.1.2. Transition rules

2.1.2.1. Rules for modelling the tick population development. For each cell at time step t , we modelled the questing tick populations as (see Table 1 for the values used and the sources of parameters):

$$qL_t = (1 - m^{qL}) \cdot qL_{t-1} + \beta \cdot 0.5 \cdot (1 - m^{AL})^{dAL} \cdot (1 - m^{fL}) \cdot (fA_{t-dAL-1}^D + fA_{t-dAL-1}^S) - fL_{t-1}^D - fL_{t-1}^S \quad (1)$$

$$qN_t = (1 - m^{qN}) \cdot qN_{t-1} + (1 - m^{LN})^{dLN} \cdot (1 - m^{fN}) \cdot (fL_{t-dLN-1}^D + fL_{t-dLN-1}^S) - fN_{t-1}^D - fN_{t-1}^S \quad (2)$$

$$qA_t = (1 - m^{qA}) \cdot qA_{t-1} + (1 - m^{NA})^{dNA} \cdot (1 - m^{fA}) \cdot (fN_{t-dNA-1}^D + fN_{t-dNA-1}^S) - fA_{t-1}^D - fA_{t-1}^S \quad (3)$$

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