



## Interplay between contact risk, conspecific density, and landscape connectivity: An individual-based modeling framework



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### ABSTRACT

In many host-pathogen systems, pathogen transmission requires close contact between infectious and susceptible hosts. The contact rates among individuals depend upon how they move in the landscape because functional connectivity can affect interactions between individuals. Yet few studies have explored the interplay between contact rates, conspecific density, and functional connectivity. Using a spatially explicit individual-based model, we investigated how empirical movement rules translate into spatial patterns of contact rates among disease hosts in complex landscapes. We developed dynamic models of functional connectivity by characterizing movement behaviors of radio-collared raccoons, which are the main hosts of the raccoon rabies virus. On this basis, we simulated space-use dynamics of raccoons in virtual landscapes varying in conspecific density, forest availability, and landscape connectivity. We then characterized spatial patterns in the density of per capita contact rates of simulated raccoons. Radio-collared raccoons were more likely to choose large habitat patches that were reached by traveling along least-cost paths, and had relatively long residence times in anthropogenic areas, especially during daytime. These movement rules that were applied to simulated raccoons in virtual landscapes revealed three key patterns in contact rates. First, few simulated raccoons were responsible for most contacts between individuals, a pattern that emerged even though all simulated raccoons obeyed the same movement rules. Second, per capita contact rates increased linearly with individual density under most conditions, which indicates that raccoon rabies transmission should be density-dependent rather than frequency-dependent. Third, functional connectivity created a broad range of patterns in the density of per capita contact rates from decreasing to increasing values, depending upon the availability of land cover types. Overall, the contacts between hosts tended to occur at highest densities in forests, anthropogenic areas, and agricultural corridors. We show that complex patterns of contact rates can emerge from simple empirical movement rules and, therefore, can be key drivers of disease spread dynamics. The strong spatial heterogeneity observed in contact rates implies that the effectiveness of particular control interventions can strongly vary depending upon host density, landscape composition, and functional connectivity. This study provides key functional relationships for tailoring interventions to changes in local conditions.

### 1. Introduction

The contact rate among individual hosts is a fundamental component for predicting the dynamics of infectious disease spread in wild populations and, thus, for developing cost-effective disease control strategies (Craft, 2015; White et al., 2017). In particular, the pathogen

transmission rate depends upon the rate at which an individual host comes into contact with another individual, and the probability that such contact is infectious (Begon et al., 2002). Simple mathematical formulations of disease transmission dynamics (McCallum et al., 2001) predict that contact rates either increase linearly with individual density in a population, resulting in density-dependent transmission

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(Anderson and May, 1979; May and Anderson, 1979), or are constant irrespective of individual density, leading frequency-dependent transmission (Thrall et al., 1993; Thrall et al., 1995). Empirical studies have shown, however, that contact rates could follow a nonlinear relationship in which contact rates increase with individual density but become saturated at high density (Habib et al., 2011; Ji et al., 2005; Ramsey et al., 2002), implying that pathogen transmission dynamics in wildlife often lie between extreme assumptions of density-dependent and frequency-dependent transmission (Smith et al., 2009). Although previous research has shown that this nonlinearity could be driven by changes in host behavior that is associated with social group ranges (Habib et al., 2011) or individual home ranges (Ramsey et al., 2002), the role of spatial heterogeneity in shaping such patterns of disease transmission remains unclear.

To optimize control interventions, quantifying variation in contact rates among individual hosts and across space is needed (Paull et al., 2011); some individuals in the landscape can have a disproportionately high number of contacts compared to the mean, which can cause “superspreading” events over large scales (Lloyd-Smith et al., 2005). For example, Woolhouse et al. (1997) proposed the 20/80 rule, wherein  $\approx 20\%$  of infected hosts (known as “superspreaders”) are responsible for 80% of infection transmission in host-pathogen systems. Although physiology and social behavior of individual hosts have been recognized as being significant sources of variation in contact rates by affecting individual susceptibility and competence (VanderWaal and Ezenwa, 2016; Wilson et al., 2002), few studies have assessed the interplay between host contact rates and landscape physiognomy (Habib et al., 2011; Kjær et al., 2008). Knowledge of the interactions between contact rates and landscape characteristics can directly inform on the likely locations of hotspots for pathogen transmission.

In human-fragmented landscapes, maintaining connectivity between habitat patches is important for biodiversity conservation (Fahrig and Merriam, 1985), but could also enhance spread and transmission of infectious diseases. For example, in the Great Plains of North America (Canada and USA), sylvatic plague (*Yersinia pestis*) is more likely to spread among colonies of black-tailed prairie dogs (*Cynomys ludovicianus*) that are spatially close together and located in close proximity to dispersal corridors (Collinge et al., 2005; Johnson et al., 2011). Landscape connectivity can affect disease transmission and spread because it determines the spatial dynamics of animal movement and the contact risk among potential hosts (Meentemeyer et al., 2012).

In landscapes where high-quality habitat patches can be delimited over space, mobile animals must decide how long to remain within a patch, where to go next, and how to get there. These decisions can strongly depend upon the structural and functional connectivity of the landscape (Courbin et al., 2014; Dancose et al., 2010). Structural connectivity describes the physical links between habitat patches, such as the Euclidean distance between them (Kindlmann and Burel, 2008; Tischendorf and Fahrig, 2000). Animals, however, do not necessarily navigate between high-quality patches along straight paths. Functional connectivity considers the adjustment of animal movements to the characteristics of the surrounding matrix (Taylor et al., 1993). Although such fine-scale movements can directly alter the contact rates between individual hosts (Koen et al., 2017; Tracey et al., 2014), only a few studies of infectious disease dynamics have considered functional connectivity (Nobert et al., 2016; Rees et al., 2013). Also, most of them provide predictions of disease occurrence, while the spatial distributions of infectious diseases depend crucially upon contact mechanisms between individual hosts (Arthur et al., 2017; White et al., 2017). Neglecting the role of contacts could affect our understanding of pathogen transmission and spread processes in heterogeneous landscapes, such that a modeling tool that would allow incorporating functional connectivity should improve the ability to anticipate the spatial dynamics of infectious diseases in wildlife populations.

Spatially explicit individual-based models (IBMs) provide a modeling framework to simulate complex dynamic systems where emergent

phenomena can be observed (Matthews et al., 2007; Railsback, 2001). In spatially explicit IBMs, individuals are represented as autonomous entities that interact with their environment and other individuals (Grimm and Railsback, 2005). The advantage of spatially explicit IBMs is that they can integrate stochastic and spatially-dependent processes at the individual level that are difficult to quantify empirically (DeAngelis and Mooij, 2005). Consequently, spatially explicit IBMs have been largely used for modeling animal movement in heterogeneous landscapes (e.g., Bauduin et al., 2016; Kramer-Schadt et al., 2004; Palmer et al., 2011; Tracey et al., 2014). Recently, Marrotte et al. (2017) have associated host movement behavior with a directional measure of landscape connectivity based on movement costs to assess contact probability between white-footed mice that are important reservoir hosts of Lyme bacteria. Prediction of contact rates, however, should also require modeling inter-patch movement decisions that consider residence time within habitat patches and choice of the next patch. The current lack of information on the functional link between contact rates, conspecific density, and landscape connectivity impedes the development of cost-effective disease control strategies.

In this study, we built a spatially explicit IBM to assess how changes in conspecific density, landscape composition, and functional connectivity alter contact rates between individual hosts. To do this, we integrated components of space use in the IBM by estimating from empirical data, residence time within high-quality habitat patches and choice of the next high-quality patch, and by simulating intra- and inter-patch movements in different virtual landscapes that differed in habitat availability and connectivity. The model has been constructed for raccoons (*Procyon lotor* L.), one of the main hosts of the raccoon rabies virus variant in North America (Finnegan et al., 2002).

## 2. Materials and methods

We developed a spatially explicit IBM that integrates three main components: 1) virtual landscapes, 2) simulated individuals representing raccoons, and 3) empirical rules of space use that are used by the simulated individuals to move across the virtual landscapes. The IBM was implemented in Netlogo (version 5.0.5; Wilensky 1999).

### 2.1. Components of the IBM

#### 2.1.1. Virtual landscapes

To assess the influence of changes in landscape composition and connectivity on per capita contact rates among individual hosts, we simulated the movement of raccoons in 15 virtual landscapes differing in terms of forest proportion and spatial configuration of agricultural corridors. In landscapes dominated by forest patches and agricultural fields, spatial distribution of raccoons is closely linked to forest cover and agricultural corridors (Tardy et al. 2015, 2014). In particular, raccoons use corridors to move between habitat patches (Beasley et al., 2007). The spatial scales used for building virtual landscapes were defined from those of agriculturally fragmented landscapes in the Montérégie region of southern Québec (Canada), where 104 rabies cases had been reported between 2006 and 2009 (Rees et al., 2011).

The virtual landscapes were represented as raster grids of  $1000 \times 1000$  cells and had an extent of 100 km<sup>2</sup>. We defined cells of  $10 \times 10$  m, which corresponds to the minimal width of agricultural corridors in the Montérégie landscapes (Tardy et al., 2014). The virtual landscapes were comprised of eight land cover types that are typical of agriculturally fragmented landscapes: forests, corn (maize) fields, other crops (including vegetable and fruit crops, together with cereal fields such as oat, wheat, soybean, hay, and barley), open-uncultivated areas, water bodies (lakes), wetlands (riparian areas around lakes), anthropogenic areas, and agricultural corridors (Fig. B1 Supplementary material). The set of adjacent cells that were composed of the same land cover type defined a habitat polygon. Each cell was identified by its centroid and was characterized by state variables referring to habitat

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