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Cross-scale modeling of a vector-borne disease, from the individual to the metapopulation: The seasonal dynamics of sylvatic plague in Kazakhstan

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ABSTRACT

Individual-based or population-level simulation approaches are often employed alternatively in ecoepidemiological modeling. In this paper, we introduce an original coupling approach applied to bubonic plague zoonotic infection in the Pre-Balkhash focus (central Asia), with main host Rhombomys opimus (Rodentia: Gerbillidae) and vector its associated ectoparasite flea Xenopsylla gerbilli minax. An Individual-Based Model (IBM) is first developed as a Multi-Agent System (MAS), addressing the seasonally forced internal dynamics of a typical burrow system based upon individual processes and interaction rules of the host-vector parasitoid system. Key population parameters and incidence functions are derived from simulations on the IBM and introduced in a second stochastic Population-Level Model (PLM), operating at the level of a metapopulation composed of interacting communities occupying burrow systems. The methodology facilitates knowledge integration and encourages bridging scales at which determinant contagion processes occur. Through simulations, we bring new insights about conditions for the local persistence of plague in a seasonally constrained environment. Under the seasonal scenario where half of the fleas overwinter in an active state, the introduction of the plague pathogen in spring in a metapopulation composed of 20 communities leads in one case out of two to epizootics surviving the first winter, while the infection has a 5% chance of passing the second winter. If the metapopulation is extended to 70 communities, simulations suggest the same 5% chance is estimated for plague persisting almost 4 years. Optimal vector community sizes or host dispersal intensities for the persistence of epizootics are also highlighted by sensitivity analyses.

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1. Introduction

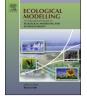
Individual-based or population-level simulation approaches are often employed alternatively in eco-epidemiology, while a major challenge in this research field is to meaningfully connect levels of organization (DeAngelis and Gross, 1992; Levin and Pacala, 1997; Matthews and Haydon, 2007; Ratzé et al., 2007; Susser and Susser, 1996). One of the main difficulties arising when using deterministic compartmental population-level models is that they rely on simplifying assumptions regarding individual diversity and the way individuals interact with each other and their environment. These assumptions are accepted by default but not always proven

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to be correct and might in some cases mistake important properties of the complex patterns modeled (Black and McKane, 2012; Breckling et al., 2005; Grimm and Railsback, 2005; Roche et al., 2011). This is so for epidemic models driven by a function of incidence involving a transmission parameter that is not based on any explicit description of the biological processes of transmission, hence being difficult to inform and sometimes considered as a fudge factor (Antonovics et al., 1995). On the other hand, individual (agent)-based epidemic models that better capture the diversity of individual behaviors and local interactions may produce more realistic patterns in a bottom-up approach. Although intuitive and flexible, they are very cumbersome and can hardly be extended to very large populations over long periods of time, nor can they be analytically explored. As a compromise to overcome the limitations and exploit the advantages of each of these modeling approaches, there is growing interest in developing hybrid modeling frameworks beyond simple model comparison (Bobashev et al.,







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2007; Fahse et al., 1998; Hilker et al., 2006; Lehnert et al., 2015). Combining dynamically individual-based and compartmental submodels into single models has recently been proposed (Banos et al., 2015; Bradhurst et al., 2015, 2013; Vincenot and Moriya, 2011) for multiscale simulation of epidemics. Vincenot et al. (2011) suggested a concept of dynamic switching between the two modeling approaches, further developed by Gray and Wotherspoon (2015, 2012). Here we propose a knowledge-driven modeling framework linking two distinct models in a static way, recalling the methodology followed by Wilson (1998). In this framework, an Individual-Based Model (IBM) is used to parameterize a stochastic Population-Level Model (PLM). The latter is hence informed by the former and enables us to make robust predictions at the population level. The modeling framework is applied to the epidemiological context of bubonic plague in the Pre-Balkhash focus (southeastern Kazakhstan), as part of the Central Asian desert natural plague focus. Bubonic plague is a zoonotic infection that circulates in wild rodents but is transmissible from them to humans through the bites of infected fleas. It is widespread in the world today and represents a continuing threat (Stenseth et al., 2008). In the Pre-Balkhash focus the great gerbil Rhombomys opimus is the main reservoir host (Aikimbajev et al., 2003; Anisimov et al., 2004; Gage and Kosoy, 2005; Pollitzer, 1966). Davis et al. (2004) proposed that the familyoriented population structure of the great gerbil and its associated ectoparasite fleas of genus Xenopsylla, along with their seasonally constrained weather-dependent dynamics, is a key factor that determines plague epizootics and plague long-term persistence in rodents in this focus. Yet, the question of the geographical scale of plague endemicity, i.e. whether plague can persist over a long time period in a local autonomous *micro-focus* – or *hotspot* – of minimum size to be determined or necessarily operates at a larger scale, remains poorly understood (Pollitzer, 1954; Schmid et al., 2012). Simulation techniques have increasingly become an essential way, complementary to statistical techniques particularly in the case of lack of field data, to provide insights about disease spread through spatially structured populations and to guide health authorities with epidemic outbreak predictions. Yet, dynamical models developed so far applied to bubonic plague do not represent explicitly as state variables or discrete entities the two populations, host and vector, involved in the transmission cycle together with their seasonally constrained dynamics (Dubyanskiy et al., 2012; Gascuel et al., 2013; Keeling and Gilligan, 2000; Laperrière et al., 2009; Schmid et al., 2012) except Foley and Foley (2010). The two models we propose here to chain allow the incorporation of the hierarchical structure of populations of gerbils and their associated fleas, from the individual level to the metapopulation level. The theory of metapopulation, originally from ecology (Hanski, 1998; Levins, 1969), has been successfully applied to vector borne-disease modeling (Adams and Kapan, 2009; Arino et al., 2012; Auger et al., 2008; Moulay and Pigné, 2013) to better capture the spatial structure of epidemics not considered in the standard well known Ross-McDonald model (Anderson and May, 1992; MacDonald, 1952; Ross, 1911). As considered in previous studies of plague in Kazakhstan (Davis et al., 2007; Schmid et al., 2012), the metapopulation refers here to interacting great gerbil family groups and their nidiculous parasites, each of one occupying a permanent burrow system with one main entrance. The subpopulations are linked to each other by an explicit exchange of individuals due to movements of great gerbils.

2. The modeling chain

In light of this hierarchical organization, two models have been developed and coupled in an original static way, as a modeling chain. A first spatially explicit individual-based model addresses the seasonally forced demographics of burrow systems as well as their internal infection dynamics, based upon individual processes and pairwise interactions of the host-vector parasitoid system. A second stochastic Population level Model captures plague propagation between burrow systems, added to within-burrow-system transmission. Parameterizing a PLM is often a difficult task either because parameters are badly informed or because they refer to a combination of unclear processes and therefore are not measurable (Fahse et al., 1998; Hilker et al., 2006). Typically, transmission terms are described on the basis of a contact rate combining a multitude of epidemiological, environmental, social and behavioral processes, not explicitly modeled. Conversely, the IBM developed here incorporates explicitly the spatial distribution, movements and encounters of individuals. Moreover, the literature does not report the fertility and mortality of fleas and gerbils as population rates per unit of time, while the wider set of individual parameters that determine seasonal population dynamics are well known and integrated into the IBM. Hence, the coupling methodology we propose here between the two models consists in deriving from simulations performed on the IBM some time series for population parameters (birth, death, dispersal) as well as the incidence functions needed in the PLM. Once those elements incorporated, the latter is then run separately in a second step to investigate conditions for the persistence of plague in the whole metapopulation.

3. The individual-based model

The Individual-Based Model (IBM) is a Multi-Agent System developed using the object-oriented Netlogo modeling platform (Wilensky, 1999). The model description follows the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2010, 2006)

3.1. Overview

3.1.1. Purpose

The IBM is designed as a state-of-the-art model which attempts to formalize simply but adequately the life cycle of individuals as well as the transmission cycle of plague pathogen in a seasonally constrained 2D environment. It assimilates a valuable amount of knowledge gained from field observations over past decades about the essential mechanisms that are at work to produce complex disease patterns. In this paper we use the IBM to derive, according to seasonal scenarios, demographic time series for hosts and vectors as well as the incidence functions addressing the dynamics of the infection within a typical burrow system.

3.1.2. Entities, state variables, and scales

Two classes of individuals are distinguished, great gerbils and fleas, distributed on a 2D grid of spatial cells (see class diagram in Appendix A1 of Supplementary material). Some of them represent burrow systems' entrances and are assumed randomly distributed. Time is modeled as discrete steps. One basic time step represents one hour, even though some procedures are executed on larger time steps. One spatial cell represents 2.5 m². Any entity, whether host or vector, is characterized by a set of state variables relating to its sex, age, infection or activity status and a set of internal time counters.

3.1.3. Process overview and scheduling

Individual processes and interactions are formalized as procedures and include, listed in the order of execution in a time step: disease transmission between fleas and gerbils, the diurnal foraging activity of great gerbils during a specified time slot, disease progress in individuals, fertility, growth and mortality of both fleas and great Download English Version:

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