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Invasion speeds of *Triatoma dimidiata*, vector of Chagas disease: An application of orthogonal polynomials method

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HIGHLIGHTS

- A structured integrodifference equation is used to study invasion speed of *T. dimidiata*.
- Importance of seasonal dispersal when estimating the invasion capacity of triatomines.
- An efficient control may be to disturb the transition from juvenile to adult stage.

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ABSTRACT

Demographic processes and spatial dispersal of *Triatoma dimidiata*, a triatomine species vector of Chagas disease, are modeled by integrodifference equations to estimate invasion capacity of this species under different ecological conditions. The application of the theory of orthogonal polynomials and the steepest descent method applied to these equations, allow a good approximation of the abundance of the adult female population and the invasion speed. We show that: (1) under the same mean conditions of demography and dispersal, periodic spatial dispersal results in an invasion speed 2.5 times larger than the invasion speed when spatial dispersal is continuous; (2) when the invasion speed of periodic spatial dispersal is correlated to adverse demographic conditions, it is 34.7% higher as compared to a periodic dispersal that is correlated to good demographic conditions. From our results we conclude, in terms of triatomine population control, that the invasive success of *T. dimidiata* may be most sensitive to the probability of transition from juvenile to adult stage. We discuss our main theoretical predictions in the light of observed data in different triatomines species found in the literature.

1. Introduction

Chagas disease, also known as American trypanosomiasis, is a life-threatening illness caused by the protozoan parasite, *Trypanosoma cruzi*. The disease is endemic in Latin America where *T. cruzi* is primarily transmitted by blood-sucking triatomine bugs (Gourbière et al., 2012), and is now spreading outside of its ancestral geographic range because of increasing international exchanges (Pinto Dias, 2013; Tanowitz et al., 2011).

As an efficient vaccine is still lacking and as it is difficult to deliver medicinal drugs in time (during and shortly after the acute stage of the disease) vector control and blood screening are the main strategies to control the transmission of this disease. Despite the important successes of the national and international control programs launched in the 90s (Abad-Franch et al., 2013), neither the 2005 target of interruption of the transmission of the disease set by the World Health Assembly in 1998, nor the 2010 target for elimination were met (Gürtler et al., 2008).

The evolution of disease transmission indeed lead to new challenges, which currently include the emergence of Chagas disease in regions previously considered to be free of the disease,

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such as the Amazon basin (WHO, 2010), the re-emergence of the disease in regions where control of key domiciliated species, such as *Triatoma infestans*, had been achieved (Gurevitz et al., 2012; Gürtler et al., 2009), and the increasing awareness that non-domiciliated species, such as *T. dimidiata* (Gourbière et al., 2008; Nouvellet et al., 2011) or *Rhodnius prolixus* (Guhl et al., 2009; Hashimoto and Schofield, 2012) can contribute to substantial levels of infection prevalence in humans (Nouvellet et al., 2013; Rascalou et al., 2012).

To deal with such challenges requires a good understanding of the triatomines' demographic and dispersal potentials, and their response to the ongoing environmental changes. The dispersal of triatomines appears as one of the less documented traits, although the ones influencing the rate of flight initiation and its direction have been investigated in the past (Galvão et al., 2001; Minoli and Lazzari, 2006; Pacheco-Tucuch et al., 2012; Schofield et al., 1991), and dispersal distances have recently been estimated more accurately by combining data on insects' spatial distribution and spatial modeling in *T. dimidiata* (Nouvellet et al., 2015). Still, some of the relationships between the demographic/dispersal life-history traits and the invasion capacity of vectors that are spreading into new geographic areas and/or the speed at which they do so, remains to be quantified.

To establish such a quantitative link requires a stage structured spatial modeling to account for the demographic and dispersal specificities of pre-adult and adult triatomines. Spatially explicit models (Dunning Jr. et al., 1995) can be used in this context in view of the geographic nature of the spread of triatomines, see (Nouvellet et al., 2015) for a review on these models and other mathematical models of Chagas disease. The geographic habitat can be modeled in a discrete or in a continuous way. Some common discrete spatio-temporal models as cellular automata (Cissé et al., 2016; Crawford et al., 2013; Slimi et al., 2009), grid-based models (Barbu et al., 2010) and based agent models (Devillers et al., 2008; Yong et al., 2015) have been used to study triatomine or *T. cruzi* invasion of domestic (e.g., (Barbu et al., 2011; Slimi et al., 2009)) and sylvatic areas (Crawford et al., 2013). Examples of spatially explicit continuous models which have been widely used to study the spread of populations and epidemics are based on reaction-diffusion (Petrovskii and Li, 2006; Skellam, 1951), integrodifferential (Medlock and Kot, 2003; Mollison, 1977) and integrodifference (Kot and Schaffer, 1986; Shigesada and Kawasaki, 2002) equations.

The work of Crawford et al. (2013) seems to be the only published work treating invasion speed of Chagas disease. In biological models, the term “invasion speed” (see Appendix A.6 for definition) is generally associated with the speed at which a certain population or infection expands over space. In (Crawford et al., 2013) a two dimentional deterministic cellular automaton (CA) model in the form of a dynamical system with 9376 equations is developed in order to study invasion of a hypothetical strain of *T. cruzi* through the region defined by the primary sylvatic cycles in northern Mexico and parts of the southeastern United States. Hosts are racoons and woodrats which are assumed not to disperse. Vectors are *Triatoma gerstaeckeri* and *T. sanguisuga* which are assumed to disperse during a maximum of 5 weeks. In this (CA) model, the invasion speed of the epidemic has been defined using two distinct methods and examined under different vector migration scenarios.

In this study we use for our modeling a structured integrodifference equation (SIDE) which offers an ideal mathematical framework to model invasions of populations in a constant (Li et al., 2005; Lui, 1989; Neubert and Caswell, 2000), and periodic or stochastic environment (Caswell et al., 2011; Schreiber and Ryan, 2011). Interestingly, under some assumptions (relying on the so called the linear conjecture), the rate of invasion of a nonlinear SIDE is approached by the rate of invasion of the linear SIDE obtained from the nonlinear SIDE at low densities and is given by an explicit formula (Caswell et al., 2011; Neubert et al., 2000; Schreiber and Ryan, 2011). This formula can also be obtained for a linear SIDE by using an approximation method, called the saddle point (or the steepest descent) method (Radcliffe and Rass, 1997). The saddle-point method is a method used to approximate some specific integrals depending on one parameter when this parameter is large (Murray, 1984). Recently, it was used in (Kot and Neubert, 2008) to analyze the linear unstructured integrodifference equation (UIDE) that models the growth and spread of populations released at the origin in one and two dimensional space: formal solutions were written to the model using the exponential transform and, by the steepest descent method, the asymptotic approximation to the solutions for long times was determined. Moreover, from this approximation, they derived a pair of equations of the rate of invasion which are equivalent to the earlier formulation given by Weinberger (1982). Kot and Neubert (2008) concluded that the saddle-point approximation was excellent not only for long times but also for all times except (possibly) the first few iterations. The steepest descent method has also been applied to infinite-dimensional matrix integrodifference equations (Powell et al., 2005), and used to obtain the speed of propagation for certain continuous time models when the spatial aspect is described by contact distributions (Radcliffe and Rass, 1984). While mathematical expressions of the variation of abundance in space and time have been derived for the linear unstructured case (Kot and Neubert, 2008), such theoretical results remain to be derived for a linearly structured model.

The first aim of this paper is to study the invasion capacity of *T. dimidiata* by calculating its invasion speed and its abundance over time and space in a sylvatic setting by considering different biological situations. We choose this species since data are available in the literature on both its demographic and dispersal parameters (see references above). The dispersal of *T. dimidiata* adults is described by a Laplace kernel in order to account for the long distances traveled by triatomines in their sylvatic biotope (Schofield et al., 1991, 1992).

Our second objective is to propose an original method that relies on orthogonal polynomials to allow calculating both abundances and invasion speed.

We set up a deterministic linear SIDE model with the triatomine population classified in two stages (juveniles and adults) that accounts for their demography and dispersal (in the biological situations considered it is assumed that only adults disperse) in a one dimensional and homogeneous habitat. This model is denoted by 2SIDE. As the density of triatomines and their rates of invasion are important pieces of information, e.g. to manage vector control, we follow here the steps of Kot and Neubert (2008) for the 2SIDE which provides, at the same time, a theoretical extension of the ideas of Kot and Neubert (2008) to a two stages SIDE. This theoretical extension is presented in Appendix A (Section A.3) and it is exemplified by considering two cases: "constant dispersal" and "periodic dispersal". General mathematical results about these two cases are given in Section 2, and detailed analyses are reported in Appendices A and B. The triatomine population densities over time and space can be represented formally by an exponential transform and a specific polynomial set, called orthogonal polynomials which are characterized by a three-term recurrence relation (TTRR) (Chihara, 1978; Szegö, 1975). Then, by the asymptotic behavior of these orthogonal polynomials and the saddle-point method, we determine approximations of the densities for long time periods from which invasion speed formulae can be obtained (see Appendices A and B). The conditions of application to the species *T. dimidiata* are given in Section 3. Specifically, a gradient of biological situations, ranging from the most favorable to the least