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Mathematical modelling of spatial sorting and evolution in a host–parasite system

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HIGHLIGHTS

- We model the evolution and spatial distribution of traits in cane toad and lungworm populations.
- We incorporate life-history trade-offs affected by these traits and examine the resulting spatial distribution of traits.
- The model predicts prepatent period and larval size of parasites evolve according to host densities, which matches previous empirical studies.
- The host wavespeed generated matches data on the invasion history of cane toads in Australia.
- Reproductive or survival disadvantage is likely to be small for strong spatial sorting to occur.

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ABSTRACT

There have been numerous empirical and agent-based modelling studies on the spatial self-structuring of traits, particularly in regard to dispersal ability (termed spatial sorting) of cane toads in northern Australia, but few mathematical modelling studies. In this study, we formulate a reaction–diffusion based partial-integro-differential equation model based on an earlier model by Bouin et al. (2012) to examine this spatial self-structuring of traits in both a cane toad population and lungworm parasite population, which evolves with the cane toad population. In particular, the traits we focus on are dispersal ability for the cane toad population and both prepatent period and larval size for the lungworm parasite population. Apart from the spatial self-structuring of these traits, our results confirm a number of observations made in empirical and agent-based studies; particularly, that there is a noticeable lag between the host and parasite population which is critically dependent on the parasite functional response to host densities, that older populations regress back to lower dispersal speeds and that spatial sorting can still occur with a disadvantage in reproductivity and/or survival in more motile individuals. Moreover, we find that such a disadvantage in reproductivity and/or survival is unlikely to be large if spatial sorting is to have a noticeable effect on the rate of range expansion, as it has been observed to have over the last 60 years in northern Australia.

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1. Introduction

A phenomenon that is often observed in biological invasions is an accelerating rate of range expansion. The current literature suggests that in many cases this is due to increased dispersal ability at the leading front of the invasion caused by “spatial sorting”, whereby heritable traits that enhance rates of dispersal accumulate at the leading front. This leads to increased rates of dispersal in successive generations due to interbreeding and produces offspring at the front with higher mean dispersal rate (Shine et al., 2011). Spatial sorting has

been observed in many populations, such as cane toads (Phillips et al., 2006), butterflies (Hughes et al., 2007) and bush crickets (Simmons and Thomas, 2004). Shine et al. (2011) further asserted that such a phenomenon allows individuals with higher rates of dispersal to invade even if they do not necessarily exhibit a greater lifetime reproductive success than their competitors, in contrast to the theory of classical natural selection. Although this has not been theoretically confirmed, both mathematical and agent-based models have provided results that support this hypothesis (Shine et al., 2011; Phillips et al., 2008; Bouin et al., 2012). While the majority of studies have concentrated on examining the spatial sorting of traits of free-living organisms, there is likely to be an influence on selective pressures on life-history traits in parasites infecting hosts undergoing spatial sorting. This is due to rapidly evolving parasite life-history strategies according to host densities; for example, at low host densities, there

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should be a strong selection pressure for traits which maximize the probability of transmission, although trade-offs with other parasite traits imply that the optimal life-history strategy varies with host densities.

The cane toad (*Rhinella marina*) in northern Australia and lungworm nematode *Rhabdias pseudosphaerocephala*, a common parasite of cane toads, are a well-studied example of such a host–parasite system. Cane toads are a highly successful invasive species in the various areas it has been introduced (e.g. Fiji, New Guinea, Philippines and various island countries in the Caribbean), usually for the purpose of controlling damage to crops by pests. Their invasion in northern Australia has been no exception; since its introduction in 1935, as an attempt to control damage in sugarcane crops in Queensland, the cane toad invasion front has accelerated with time due to spatial sorting. Current estimates place the speed of the moving front at 55–60 km/year with the front having passed the border into Western Australia in 2009 (Shine, 2010; Brown et al., 2014).

Rhabdias pseudosphaerocephala is the most common lung parasite in Australian cane toads, with over 80% prevalence in a sample of 580 toads in a study by Barton (1998). The toads at the invading front lack the parasite due to low transmission rates at low host densities; this has resulted in the parasite invading front lagging behind its host's by approximately 2 years. The parasite exhibits a direct life-cycle; infective larvae invade a cane toad through the skin or alimentary tract and enter the lungs, where they feed on the host and mature. Eggs released in the lungs are passed onto the digestive tract where they hatch and enter the soil with the host faeces which completes the life-cycle. *Rhabdias pseudosphaerocephala* also exhibits spatial sorting in the form of life-history traits rather than dispersal ability. This is due to the rapid evolution of life-history traits associated with transmission and survival in response to changing host densities. In particular, low host densities at the invading front should favour the selection of variations in life-history strategies which enhance the parasite's ability to successfully infect hosts and reproduce. This was evidenced by Kelehear et al. (2012) who compared life-history traits among different lungworm populations, suggesting that those at the range edge exhibited larger eggs, larger free-living adults and larger infective larvae, due to increased parasite juvenile mortality at the range edge, and reduced prepatent period (reduced age at maturity). This is presumably a form of life-history trade-off; large larvae have higher establishment success but maternal fitness at high host densities is maximised by producing many small offspring even though their establishment success is lower. Similarly, parasites with shorter prepatent period exhibit reduced longevity and lifetime fecundity.

Mathematical modelling of accelerating dispersal, such as in the case of the cane toads, has received increasing attention over the recent years. It is well known from mark-recapture studies that many populations disperse according to a leptokurtic (fat-tailed) dispersal kernel as opposed to a Gaussian dispersal kernel, as is commonly assumed in modelling studies. Such fat-tailed dispersal kernels have been attributed to population heterogeneity and can generate an increased probability of long-distance dispersal, which can in turn generate accelerating dispersal (Stover et al., 2014; Hastings, 2005). They have been the main ingredient of various models, such as integro-difference equations and fractional reaction-diffusion models (Kot et al., 1996; Baeumer et al., 2008). However, these models intrinsically include a fat-tailed dispersal kernel, without modelling the population heterogeneities which generate the kernel. Moreover, they assume a fixed dispersal kernel, whereas in reality it is likely to be changing over time. It is only until recently that there has been focus on spatial sorting as a source of the leptokurtosis (see Phillips et al., 2008; Perkins et al., 2013; Stover et al., 2014).

In this study, we examine the spatial variation of fitness traits of both a host and parasite, where we use the cane toad and lungworm

R. pseudosphaerocephala as a specific example of such a host–parasite system. We formulate a partial integro-differential equation (PIDE) model, accounting for traits influencing dispersal ability for the cane toads and prepatent period and larvae size for the lungworms. Firstly, we qualitatively and quantitatively examine the acceleration of the cane toad invading front due to spatial sorting, and how this varies with trade-offs in survival and reproduction associated with increased dispersal ability. Secondly, we qualitatively examine the variation in life-history traits of the lungworm population emerging from the host undergoing spatial sorting and determine how this variation is influenced by host densities. Although there have been previous agent-based modelling studies done on this problem, to our knowledge this is the first PIDE model in the literature which describes the evolution of life-history traits in this specific host–parasite system. Note that we do not examine whether the lungworm nematode *Rhabdias pseudosphaerocephala* is a suitable biological control for the cane toad invasion; instead, we focus on the interplay between the evolutionary and spatial dynamics of the host–parasite system, and compare with observations made in previous empirical studies.

2. Model formulation

Denote the host and parasite population density at position x and time t by $u(x, \theta, t)$ and $v(x, a, \gamma, t)$, where $\theta \in [0, 1]$ is a measure of dispersal ability, $a \in [0, 1]$ is a measure of parasite larval size and $\gamma \in [0, 1]$ is a measure of the parasite prepatent period. We assume that parasite larval size is positively correlated with survivability in the environmental stage of the parasite lifecycle and negatively correlated with number of offspring produced. We model spatial movement using a reaction–diffusion system where the spatial diffusion coefficient is dependent on the dispersal ability of the cane toad. The mutation of the life-history traits θ , a and γ are modelled with diffusion terms, where the diffusion coefficient for these diffusion terms is assumed to be constant. We assume that if there is an absence of hosts, then there will be an absence of parasites at a particular x position, that is, if $\int_0^1 u d\theta = 0$ then $\int_0^1 \int_0^1 v da d\gamma = 0$ for a particular x . This is equivalent to assuming that the dispersal rate of the parasites is directly tied with the dispersal rate of the cane toads. We denote the spatial diffusion coefficient for the cane toads by $f(\theta)$ (defined in Section 3) and define the spatial diffusion coefficient for the parasite population by the normalised average of $f(\theta)$, that is, $\frac{\int_0^1 f(\theta)u d\theta}{\int_0^1 u d\theta}$. Note that we

have set $\lim_{u \rightarrow 0} \frac{\int_0^1 f(\theta)u d\theta}{\int_0^1 u d\theta} = 0$ as this is the biologically relevant choice for the limit.

For the cane toad population, we assume logistic growth with the assumption of homogeneous mixing. We denote the reproductive rate r_h and mortality rate μ_h and let them be functions of θ . Throughout this study, we only consider $r_h(\theta)$ and $\mu_h(\theta)$ to be non-increasing and non-decreasing respectively with a linear relationship in θ , representing a cost in enhanced dispersal. They are given by

$$r_h(\theta) = \bar{r}_h(1 - c\theta), \quad (2.1)$$

$$\mu_h(\theta) = \bar{\mu}_h(1 + d\theta). \quad (2.2)$$

Similar to the equation for cane toads, we denote the reproductive rate and mortality rate of the parasites by r_p and μ_p respectively. These are defined such that the following trade-offs, mentioned in Section 1, are captured in the dynamics:

1. Low host density selects for low γ (prepatent period) and vice versa.

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