Ecological Complexity 26 (2016) 6–20

Contents lists available at ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom

Original Research Article

Assessment of rabbit hemorrhagic disease in controlling the population of red fox: A measure to preserve endangered species in Australia

Parimita Roy, Ranjit Kumar Upadhyay *

Department of Applied Mathematics, Indian School of Mines, Dhanbad, Jharkhand 826 004, India

ARTICLE INFO

Article history:
Received 28 July 2015
Received in revised form 10 December 2015
Accepted 21 January 2016
Available online 15 March 2016

Keywords:
Vulpes vulpes
Conservation
Functional response
Bifurcation analysis
Cross-diffusion

ABSTRACT

Predator's management requires a detailed understanding of the ecological circumstances associated with predation. Predation by foxes has been a significant contributor to the Australian native animal reduction. This paper mainly focuses on the dissemination of rabbit hemorrhagic disease in the rabbit population and its subsequences on red fox (*Vulpes vulpes*) population, by qualitative and quantitative analyses of a designed eco-epidemiological model with simple law of mass action and sigmoid functional response.

Existence of solution has been analyzed and shown to be uniformly bounded. The basic reproduction number (R_0) is obtained and the occurrence of a backward bifurcation at $R_0 = 1$ is shown to be possible using central manifold theory. Global stability of endemic equilibrium is established by geometric approach. Criteria for diffusion-driven ecological instability caused by local random movements of European rabbits and red fox are obtained. Detailed analyses of Turing patterns formation selected by reaction-diffusion system under zero flux boundary conditions are presented. We found that transmission rate, self and cross-diffusion coefficients have appreciable influence on spatial spread of epidemics. Numerical simulation results confirm the analytical finding and generate patterns which indicate that population of red foxes might be controlled if rabbit hemorrhagic disease (RHD) is introduced into the rabbit population and thus ecological balance can be maintained.

1. Introduction

In mid 1870s, the intrusion of the European red fox had a devastating effect on Australian native wildlife species and simultaneously on the environment. The red fox is the most widespread terrestrial carnivore (Harris and Baker, 2001) which is largely distributed in the whole world. *Vulpes vulpes* are the largest species of the genus Vulpes and is commonly known as European red fox which was intruded into Australia for recreational hunting purposes. The red fox diet consists mainly of rabbits, small rodents, insects, small birds, wild berries and fruits (Ables, 1975; Jameson and Peeters, 1988). They are said to be '*opportunistic feeders*' meaning that the amount of food consumed is dependent on supply (Ables, 1975) only. There are two subspecies of foxes present in California (i) *Vulpes vulpes necator*, and (ii) *Vulpes vulpes fulva*. The red fox manifest ingenious hunting behavior and its ideal food is the rabbit population because of its size and ease of availability (Amores, 1975). Thus, foxes apparently behave as a facultative predator in their consumption of rabbits with a specialization in rabbits when they are abundant and a shift to other prey when rabbits are scarce.

Over the past 65 years, rabbit populations have dramatically reduced as a result of the arrival of two viral diseases (Villafuerte et al., 1995): (i) *myxomatosis* in 1950s and (ii) rabbit hemorrhagic disease (RHD) in the end of 1980s. Looking into this fact, RHD has been introduced in Australia as a bio-control agent, where rabbits are a major pest species. Apart from this there is another benefit of controlling rabbits in Australia such as the decline of *Vulpes vulpes* and *Feliscatus* (Williams et al., 1995; Newsome et al., 1997). European foxes are serious threat to many birds, mammals, reptiles and amphibian population and predation by them was listed as a key threatening process (Dickman et al., 1993; Smith and Quin, 1996). Saunders et al. (1995) have suggested that at least 20 species of Australian mammals become extinct and further 43 species are either endangered or vulnerable. This wave of extinctions is still continuing (Wheeler and Priddel, 2009).

* Corresponding author. Tel.: +91 326 2235482; fax: +91 326 2296563.
E-mail address: ranjit.chaos@gmail.com (R.K. Upadhyay).

http://dx.doi.org/10.1016/j.ecocom.2016.01.002
1476-945X/

Controlling European wild rabbit through baiting which dominate the dietary source of foxes in Australia can be one of the salient steps to halt this series of extinction. Morton (1990) reviewed the processes that led to the decline and extinction of many vertebrate species in Australia. Although, he ranked the role of introduced predators as secondary in the demise of native species. However, an analysis of bounty payments during 1883–1920 suggested that the predation by foxes caused the extinction of three bettongs species and other species in New South Wales (Short, 1998). This view was supported by Pech and Hood (1998) whose model suggested that the existence or recovery of declined species is strongly influenced by their exotic predators such as foxes. Holden and Mutze (2002) also studied the impact of RHD on population dynamics and diet of foxes and feral cats in the Flinders Ranges, South Australia. They found that when rabbit numbers were reduced to 85% after the advent of RHD, both the species decreased. Using these revealed facts, we designed an eco-epidemiological model system consisting of rabbit population (susceptible as well as infected prey) suffering from Rabbit hemorrhagic disease and red fox consuming rabbit population (as predator population).

The primary goal of this paper is to analyze and thereby identify mathematically viable condition (threshold) that determine whether predator population, red fox will reduce due to deadly rabbit disease or it will remain to grow at the same pace. We also attempted to find whether the contraction of fox can be driven by changes in the distribution of the European rabbit in Australia after the RHD introduction. We propose a new eco-epidemiological model considering RHD disease in rabbit prey population, which is consumed by generalist predator population and discuss the role of transmission rate in the context of eco-epidemiology. We have also included spatial variations while developing the model. The inclusion of spatial variables in a model can reveal a geographical trend in distribution of the red fox. We predict that the interaction of self- and cross-diffusion can be considered as an important mechanism for the appearance of complex spatiotemporal patterns in eco-ecological model. This paper is constituted as follows. In Section 2, the model is developed. Section 3 contributes to the analysis of the non-spatial system including boundedness of solutions, characteristics of possible equilibria, conditions under which the equilibria exist and are asymptotically stable. Numerical simulation for the temporal model are also presented in this section. The analysis of the spatiotemporal system is presented in Section 4. In this section, numerical simulation in two dimensional space is also performed. In the final section, we interpret our results in terms of their ecological implications.

2. The development of eco-epidemiological model system

Pech and Hood (1998) constructed a model for rabbit-fox dynamics to study the consequences of rabbit calivirus disease (introduced as a bio-control agent for rabbits in Australia) on fox population. Newsome (1995) developed a socio-ecological model for red fox populations subjected to fertility control in Australia. Development of our model considers the fact that wherever rabbits are common they form the major staple food for red foxes. Red foxes consume few rabbits at low rabbit densities, they increase the consumption of rabbits at intermediate densities (density-dependent response) and this consumption approaches an asymptote at high rabbit densities (Boutin, 1995). Holling type III responses have been frequently associated with predation switching by generalist consumers (Andersson and Erlinge, 1977; Hansson and Henttonen, 1985). Pech et al. (1992) showed that a Holling Type III functional response fitted the dietary data and was consistent with the observed dynamics of an eruptive rabbit population. Delibes-Mateos et al. (2008) investigated the feeding responses of the red fox to different densities of European wild rabbit (*Oryctolagus cuniculus*) in central-southern Spain and showed that the feeding pattern of the red fox is closer to a Holling type III response. We also hypothesize that feeding patterns of red foxes approximate to Holling type III functional response, typical of generalist predators (Holling, 1959; Pech et al., 1992; Delibes-Mateos et al., 2008). The disease is spread among the prey population and is not genetically inherited as rabbits less than 2 months are unaffected by the virus (Moss et al., 2002). The disease spreads horizontally with mass action incidence rate βSI. There is no recovery for the infected rabbit (prey) population and the infected rabbit dies before recovery i.e. the infected prey population cannot recover or become immune. We also assume that the predators cannot distinguish between infected and susceptible populations, so that predator species consumes the prey species (susceptible as well as infected) according to the Holling type III functional response. We have considered only one prey because we want to study the impact of disease RHD (introduced deliberately in Australian rabbit population as a bio-control agent) on the red fox population. We assume that the generalist predator does have an alternative food supply which is considered to be constant or static. This is obviously a simplification of reality, since generalist predators can often choose between a numbers of different preys and consumption of these alternative preys can drastically change their densities and strongly influence the model prediction. In few existing works (Roy and Chattopadhyay, 2005; Haque and Venturino, 2006, 2008) in which the predator was suggested to be a generalist, the alternative food supply was always considered to be constant (fixed), i.e. to be static. Recently, Venturino (2016) (see references therein) also mentioned that most models in theoretical eco-epidemiology make the important assumption that the predator consumes only one prey species.

With the above assumptions, we describe the following set of autonomous non-linear differential equations

$$\frac{dS}{dt} = rS\left(1-\frac{S}{K}\right)-\beta SI-\frac{\omega_1 S^2 P}{S^2+d_1}-\eta S = Sg_1(S,I,P) = f_1(S,I,P), \tag{1a}$$

$$\frac{dI}{dt} = \beta SI-\frac{\omega_2 I^2 P}{I^2+d_1}-\gamma I = Ig_2(S,I,P) = f_2(S,I,P), \tag{1b}$$

$$\frac{dP}{dt} = \frac{\omega_3 S^2 P}{S^2+d_1}+\frac{\omega_4 I^2 P}{I^2+d_1}-cP = Pg_3(S,I,P) = f_3(S,I,P), \tag{1c}$$

with $S(0) = S_0 > 0$, $I(0) = I_0 > 0$ and $P(0) = P_0 > 0$.

All the parameters r, K, η, β, γ, ω_1, ω_2, ω_3, ω_4, d_1 and c are positive constant. r, K and β represents intrinsic birth rate, environmental carrying capacity and transmission rate or the force of infection respectively. (ω_1, ω_2) represent the maximum predation rates, and (ω_3, ω_4) represent the conversion rates of S and I respectively, d_1 measures the extent to which the environment provides protection to rabbit population. η represents the death rate of susceptible rabbit population due to human activities like hunting and poisoning and γ represent the total death rate of infected rabbit population due to disease. c is the total death of predator population (see Fig. 1).

Further, we also assume that both the prey and predator population perform active movements in x and y directions and are biologically relevant. Random movement of animals occurs because of various requirements and necessities like, search for better food, better opportunity for social interactions such as finding mates (Okubo and Levin, 2001). In population dynamics, it makes sense to introduce side effects like population pressures created by predators. In order to show the effect of cross-diffusion to the system (1a)–(1c), and assuming that the prey and predator