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Spatiotemporal epidemic models for rabies among animals☆

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ABSTRACT

Rabies is a serious concern to public health and wildlife management worldwide. Over the last three decades, various mathematical models have been proposed to study the transmission dynamics of rabies. In this paper we provide a mini-review on some reaction-diffusion models describing the spatial spread of rabies among animals. More specifically, we introduce the susceptible-exposed-infectious models for the spatial transmission of rabies among foxes (Murray et al., 1986), the spatiotemporal epidemic model for rabies among raccoons (Neilan and Lenhart, 2011), the diffusive rabies model for skunk and bat interactions (Bonchering et al., 2012), and the reaction-diffusion model for rabies among dogs (Zhang et al., 2012). Numerical simulations on the spatiotemporal dynamics of these models from these papers are presented.

1. Introduction

Rabies is an acute, viral, and fatal zoonotic disease to mammals. It remains an important threat to public health and a concern of wildlife management worldwide. Human rabies still causes thousands of deaths annually in Asia and Africa (Fooks et al., 2014; Wunner & Briggs, 2010), and dogs are responsible for most of these deaths (CDC, 2011; WHO, 2010). Rabies virus is present among various mammal species, including red fox and raccoon dog in Europe; raccoon, red fox, skunk, and insectivorous bats in North America; domestic dogs, insectivorous and vampire bats in South America; and domestic dogs, bat, Chinese ferret badger, raccoon dog, rat, fox, and wolf in Asia (Sterner & Smith, 2006; Wang, Tang, & Liang, 2014).

Rabies emerged in Eastern Europe after World War II and spread westward through the 1980s. The spread of rabies among foxes has inspired extensively studies on rabies, including mathematical modeling on analyzing the epidemiological characteristics and transmission dynamics of rabies and designing useful control measures. In a pioneer paper, Anderson, Jackson, May, and Smith (1981) developed a deterministic model consisting of three subclasses of fox, susceptible, infectious and recovered, to explain epidemiological features of rabies in fox populations in Europe. A susceptible, exposed, infectious, and recovered (SEIR) model was proposed by Coyne, Smith, and McAllister (1989), and lately was also used by Childs et al. (2000), to predict the local dynamics of rabies among raccoons in the United States. Clayton, Duke-Sylvester, Gross, Lenhart, and Real (2010) and Ding, Gross, Langston, Lenhart, and Real (2007) considered the optimal control of SEIRS models which describe the population dynamics of rabies in raccoons. Dimitrov, Hallam, Rupprecht, Turmelle, and McCracken (2007) presented a model for the immune responses to a rabies virus in bats and George et al. (2011) presented a mathematical model parametrized with data on rabies in big brown bats in Colorado. Besides these deterministic models, discrete models (Allen, Flores, Ratnayake, & Herbold, 2002; Artois, Langlais, & Suppo, 1997), individual-based models (Rushton, Shirley, MacDonald, &

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Reynolds, 2006), and stochastic models (Russell, Real, & Smith, 2006; Smith, Lucey, Waller, Childs, & Real, 2002; Smith & Wilkinson, 2003) have also been employed to study the transmission dynamics of rabies. We refer to reviews by Sterner and Smith (2006) and Panjeti and Real (2011) for more references on different rabies models.

There have been some studies on modeling canine and human rabies, see, for example, Carroll, Singer, Smith, Cowan, and Massei (2010), Hampson et al. (2007), Zinsstag et al. (2009), etc. Ruan (2017) reviewed some recent studies on modeling the transmission dynamics of human rabies in China by considering different characters and aspects.

To study the westward spread of rabies among foxes in Europe, mathematical models described by partial differential equations have been proposed. Källén (1984) and Källén, Arcuri, and Murray (1985) studied rabies transmission in fox population by differential equations with diffusion and used the deterministic model to simulate rabies epizootic in foxes crossing continental Europe and proved the existence of traveling waves. Murray, Stanley, and Brown (1986) and Murray and Seward (1992) also considered foxes rabies, calculated the speed of propagation of the epizootic front and the threshold for the existence of an epidemic, and quantified a means to control the spatial spread of the disease. Since then, spatiotemporal models have been developed to study the spatial spread of rabies among other animals. In this paper we give a mini-review on some reaction-diffusion models describing the spatial spread of rabies among animals. More specifically, we introduce the susceptible-exposed-infectious models for the spatial transmission of rabies among foxes (Murray et al., 1986), the spatio-temporal epidemic model for rabies among raccoons (Neilan & Lenhart, 2011), the diffusive rabies model for skunk and bat interactions (Borchering et al., 2012), and the reaction-diffusion model for rabies among dogs (Zhang et al., 2012). Numerical simulations on the spatiotemporal dynamics of these models from these papers are presented.

2. Spatial spread of rabies in fox (Murray et al., 1986)

Murray et al. (1986) studied the spatial spread of rabies among foxes and examined the rabies epidemic, started in 1939 in Poland and moved steadily westward at a rate of 30–60 km per year. The basic spatial model of Murray et al. (1986) is an extension of the ODE model developed in Anderson et al. (1981) by including the spatial spread of the disease, which is caused by the random dispersal of rabid foxes.

Let $S(x,t), I(x,t)$, and $R(t,x)$ denote densities of susceptible, infected but non-infectious, and infectious foxes, respectively, in the space-time coordinate (x,t). The basic model assumptions made by Murray et al. (1986) are as follows: (i) The dynamics of the fox population in the absence of rabies is approximated by the logistic growth law with the birth rate a, the intrinsic death rate b, and the environmental carrying capacity K. The seasonality of births and food supply are neglected. (ii) Rabies is transmitted from rabid to susceptible fox: interspecies transmission is neglected. Susceptible foxes become infected at an average rate per head βR, which is proportional to the number of rabid foxes present. (iii) Infected foxes become infectious at an average rate per head σ, where $1/\sigma$ is the average incubation time. (iv) Infectious foxes die at an average per capita rate α ($1/\alpha$ is the average duration of clinical disease). (v) Infected and infectious foxes continue to pressure on the environment and to die of cause other than rabies, but they have a negligible number of healthy offspring. (vi) Foxes are territorial and divide their territories up into non-overlapping ranges. (vii) Rabies is transmitted by direct contact (usually by biting) between foxes. (viii) Rabies acts on the central nervous system inducing behavioral changes in foxes. About half of infected foxes have furious rabies and exhibit the ferocious symptoms typically associated with the disease, while with the rest the virus affects the spinal cord, causing gradual paralysis. Foxes with furious rabies may become aggressive and confused, losing their sense of direction and territorial behavior, and wandering randomly. So a diffusion term is added to the equation for the infectious foxes.

The base spatial model takes the following form

$$\begin{aligned}
\frac{\partial S}{\partial t} &= (a-b)\left[1-\frac{N(x,t)}{K}\right]S(x,t)-\beta S(x,t)R(x,t),\\
\frac{\partial I}{\partial t} &= \beta S(x,t)R(x,t)-\sigma I(x,t)-\left[b+(a-b)\frac{N(x,t)}{K}\right]I(x,t),\\
\frac{\partial R}{\partial t} &= D\frac{\partial^2 R}{\partial x^2}+\sigma I(x,t)-\left[b+(a-b)\frac{N(x,t)}{K}\right]R(x,t),
\end{aligned} \tag{1}$$

where $N(x,t)=S(x,t)+I(x,t)+R(x,t)$ is the total fox population and D is the diffusion coefficient. The term $(a-b)N/K$ in each equation represents depletion of the food supply by all foxes. The dimensional parameters in (1) are given in Table 1 and are taken from Murray et al. (1986).

When $D=0$, model (1) becomes the spatial homogeneous model proposed by Anderson et al. (1981) who found that when rabies is introduced into a stable population of healthy foxes these equations predict three possible behaviors. By considering the basic reproduction number, they obtained a critical value of the carrying capacity of the system given by (see also Wang & Zhao, 2012)

$$K_c=\frac{(\sigma+a)(\alpha+a)}{\beta\sigma}.$$