

Lattice three-species models of the spatial spread of rabies among foxes

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Abstract

Lattice models describing the spatial spread of rabies among foxes are studied. In these models, the fox population is divided into three-species: susceptible (S), infected or incubating (I), and infectious or rabid (R). They are based on the fact that susceptible and incubating foxes are territorial while rabid foxes have lost their sense of direction and move erratically. Two different models are investigated: a one-dimensional coupled-map lattice model, and a two-dimensional automata network model. Both models take into account the short-range character of the infection process and the diffusive motion of rabid foxes. Numerical simulations show how

the spatial distribution of rabies, and the speed of propagation of the epizootic front depend upon the carrying capacity of the environment and diffusion of rabid foxes out of their territory.

1 Introduction

Rabies is one of the oldest recorded infectious diseases. Records from the Middle Ages show that rabies was then widespread in western Europe. Throughout the world, dogs are important vectors, however, there exist many early references to several species of wildlife implicated in the spread of the disease [1], [2], [3]. Nowadays, most cases of rabies are found among animals (dogs, cats, livestock, wildlife). According to Macdonald [3], the present European epizootic (epidemic among animals) began south of Gdansk (Poland) in 1939. Moving westwards, it was first recorded in France in 1968, the Netherlands in 1974, Spain in 1975 and Italy in 1977. Its main vector and victim is the red fox.

Rabies is an acute infectious disease of the central nervous system caused by a virus. The disease is transmitted from rabid to susceptible foxes, usually by biting. About half of the infectious foxes become aggressive, and lose their sense of direction and territorial behavior, wandering randomly.

Murray and co-workers [4], [5], [6] studied different models of the spread of rabies among foxes formulated in terms of partial differential equations. In these models, the fox population is divided into three species: susceptible, infected but non-infectious, and rabid foxes which are infectious. The principal assumptions are:

- (i) Susceptibles evolve in time according to a logistic equation.
- (ii) Susceptibles become infected at an average rate per capita proportional to the number of rabid foxes present.
- (iii) Infected foxes become rabid after an average incubation period.
- (iv) Rabid foxes die after an average duration of the disease.
- (v) Rabid and infected foxes also die of causes other than rabies.
- (vi) The spatial spread of the disease is essentially due to the random motion of the rabid foxes

Such models have unquestionably contributed to our understanding of the spread of an infectious disease, but they do not take correctly into account the short-range character of

the infection process, and neglect spatial correlations. In order to include these features, we have built up and studied two lattice models in which the spread of the epidemic is viewed as the growth of a random cluster on a lattice. We will first describe a coupled-map lattice model, and then a two-dimensional automata network model.

2 Lattice models

The spread of an epidemic in a population is a complex process. When modeling such a process, among the many features which are likely to be important, we should, however, only retain the few relevant ones which are thought to play an essential role in the interpretation of the observed phenomena. In both models, at each time step, the fox population evolves according to the following rules:

- (1) A susceptible has a probability b to give birth to a susceptible at a nearby empty location. Infected and rabid foxes do not give birth.
- (2) Susceptibles and infected have a probability d to die due to natural causes, and d_ℓ multiplied by the total local population density of neighboring foxes (*i.e.* susceptibles + infected + infectious) due to lack of food.
- (3) Susceptibles become infected at a rate proportional to the local density of neighboring rabid foxes, the proportionality factor is the probability p_i to be infected.
- (4) Infected, *i.e.* incubating, foxes become rabid with a probability p_r .
- (5) Non-rabid foxes being territorial, susceptibles and infected foxes evolve without moving to a neighboring territory.
- (6) Rabid foxes have a probability d_r to die due to the disease, and d_ℓ multiplied by the total local density of neighboring foxes due to lack of food.
- (7) Rabid foxes move at random to a neighboring location.

In order to exhibit some realistic features of the spread of a rabies epidemic, following the analysis of Murray *et al* [5], our models have to contain a minimum number of

parameters. There is one source term coming from the birth of susceptibles (parameter b). To account for the three death processes, natural causes, lack of food, and rabies, we need 3 parameters (d , d_ℓ , and d_r). We need to introduce a parameter which measures the probability to be infected by contact (parameter p_i). The existence of an incubation period is an essential feature to exhibit decreasing periodic fluctuations following the main wave front of the susceptible population (parameter p_r).

2.1 Coupled-map lattice model

A coupled-map lattice is a dynamical system in which space and time are discrete variables while states are continuous [7], [8]. Here the state of the system is represented by the function $\mathbf{P} : (i, t) \mapsto \mathbf{P}(i, t)$, where $(i, t) \in \mathbb{Z} \times \mathbb{N}$, and $\mathbf{P} \in [0, 1]^3$ is a three-dimensional vector whose components are $S(i, t)$, $I(i, t)$, and $R(i, t)$ which denote, respectively, the densities at site i and time t of susceptible, infected and rabid foxes. \mathbb{Z} is the set of all integers and \mathbb{N} is the set of nonnegative integers. In this model, each site corresponds to a specific territory. Susceptibles and infected foxes evolve without moving to a neighboring site. On the contrary, rabid foxes, which have lost their sense of direction, move to one of their two neighboring sites with equal probabilities. According to our assumptions (Rules 1 to 7), the dynamics of the system is governed by the following recurrence relations:

$$\begin{aligned}
S(i, t + 1) &= S(i, t) - dS(i, t) - d_\ell N(i, t)S(i, t) \\
&\quad + b(1 - N(i, t))S(i, t) - p_i R(i, t)S(i, t) \\
I(i, t + 1) &= I(i, t) - dI(i, t) - d_\ell N(i, t)I(i, t) \\
&\quad + p_i R(i, t)S(i, t) - p_r I(i, t) \\
R(i, t + 1) &= R(i, t) - d_r R(i, t) - d_\ell N(i, t)R(i, t) + p_r I(i, t) \\
&\quad + D(R(i - 1, t)) + R(i + 1, t) - 2R(i, t),
\end{aligned}$$

where $N(i, t) = S(i, t) + I(i, t) + R(i, t)$ is the total fox density at site i and time t , and D is the diffusion coefficient characterizing the random motion of the rabid foxes.

2.2 Automata network model

An automata network is a fully discrete dynamical system. That is, space, time and states are discrete variables. In our model, the space consists of a square $L \times L$. Since we are interested in the spread of an epidemic starting at the center of the lattice, we did not choose cyclic boundary conditions. As for a coupled-map lattice, the time variable is a nonnegative integer. The state of the system at time t is described by the function $s_t : (i, j) \mapsto s(i, j; t)$, where $(i, j) \in \mathbb{Z}_L^2$, $t \in \mathbb{N}$, and $s(i, j; t)$ can take four values corresponding to the four possible states of the site (i, j) since this site can be either empty or occupied by one of the three fox species (susceptible, infected, rabid). At each time step, the state of the system evolves according to the successive application of the two following subrules:

- first a local rule describing birth, death and infection processes, which is applied to all sites synchronously;
- then, a motion rule mimicking rabid fox erratic motion.

Subrule (1) is a probabilistic, two-dimensional, four-state cellular automaton rule, which is defined as follows. At each time step,

- (i) each susceptible has a probability b to give birth to a susceptible at an empty first-neighbor site, therefore, the probability that an empty site, having z_s susceptibles among its four first-neighbors, becomes occupied by a susceptible is $1 - (1 - b)^{z_s}$;
- (ii) each susceptible has a probability d to die of natural causes;
- (iii) each susceptible having z_i rabid foxes among its four first-neighbors becomes infected with a probability $1 - (1 - p_i)^{z_i}$;
- (iv) each infected has a probability d to die of natural causes;
- (v) each infected has a probability p_r to become rabid;
- (vi) a rabid fox has a probability d_r to die of the disease;
- (vii) each fox (either susceptible, or infected, or rabid) having z_f foxes among its first-neighbors has a probability $d_\ell z_f$ to die due to lack of food.

Subrule (2) can be described as follows: At time t , a rabid fox is selected at random to perform a move to a first-neighbor site also selected at random. If the site is empty the fox will effectively move otherwise it will not. This process is repeated $mN_R(t)L^2$, where $N_R(t)$ denotes the density of rabid foxes at time t . The parameter m represents the average number of tentative move per rabid fox at time t . Note that this sequential diffusive process allows some rabid foxes to move more than others.

Automata networks of this type are called *diffusive cellular automata*. Their general properties have been studied by Boccara *et al* [9]. They have been used to build up various epidemic models [10] in which the motion of the individuals play an important rôle in the spread of the epidemic.

3 Numerical simulations: results and analysis

3.1 Coupled-map lattice model

In our simulations, the lattice size is 441. The sites are labeled from -220 to 220 . The initial susceptible fox densities have the same value at all sites i , while the initial infected and rabid fox densities are nonzero only at the central site. These values are: $S(i, 0) = 0.6$. $I(0, 0) = 0.005$, and $R(0, 0) = 0.005$. For all $t \in \mathbb{N}$, at the boundaries of the chain, the densities of the various fox species satisfy the condition

$$S(L + 1, t) + I(L + 1, t) + R(L + 1, t) = 0$$

$$S(-L - 1, t) + I(-L - 1, t) + R(-L - 1, t) = 0$$

As reported by Macdonald [3] and Murray [6], the epidemic spread of rabies among foxes is characterized by a traveling epizootic wave front followed by periodic decreasing fluctuations of susceptibles density which tends to its steady state. Our numerical simulations show that our coupled-map lattice model clearly exhibits these features, as illustrated in Figure 1 which represents, at a given time, the variations of susceptible, and rabid fox densities, as a function of site location for two different values of d_ℓ . Increasing d_ℓ decreases the height of the peak of the first and subsequent outbreaks of infected

and rabid foxes. A smaller value of d_ℓ is equivalent to a larger carrying capacity of the environment, therefore, a larger carrying capacity implies a more severe epidemic.

Figure 2 illustrates the influence of the diffusion coefficient D . As expected, increasing D increases the speed at which the epidemic spreads (see also Figure 3). While the values of the amplitudes of the various fox densities do not change, the distance between two successive outbreaks increases with D .

According to epidemiological evidence (cf. references in Murray [6]) there exists a threshold value for the carrying capacity below which rabies die out. In the case of our model we found that for $d_\ell > 0.0456$ the epizootic does not spread (see Figure 4). This threshold depends, of course, upon the values of the other parameters.

We have determined numerically the speed of the epizootic wavefront as a function of the diffusion coefficient D for two different values of the parameter d_ℓ . Our results are represented in Figure 3. As expected from a dimensional argument, this speed varies as \sqrt{D} . Increasing d_ℓ , we verify again that the speed of the epizootic wavefront decreases.

We have also determined numerically the speed of the epizootic wavefront as a function of the parameter d_ℓ . Figure 4 shows that, as we already mentioned, this speed is a decreasing function of d_ℓ , which goes to zero at a threshold value.

3.2 Automata network model

In our simulations, the lattice size is 201×201 . Simulations start from a random initial configuration. The initial densities of susceptible, infected and rabid foxes are, respectively, equal to 0.6, 0.005, and 0.005. Rabid and infected foxes exist only inside a disk of radius 10 in the initial configuration. Our results are averages over 50 to 100 different initial configurations.

As for the coupled-map lattice model, we have studied the influence of the carrying capacity and the diffusion on the various fox species. We found similar results as illustrated in Figures 5a-5c. Increasing d_ℓ decreases the height of the peak of the first and subsequent outbreaks of rabid foxes (Figures 5a and 5b), while increasing m increases the speed at which the epidemic spreads (Figures 5b and 5c). Above a threshold value of d_ℓ , which is equal to 0.053 for $m = 0.5$ and 0.0245 for $m = 0.1$, the epizootic does not spread (see

Figure 9).

As time increases, rabid foxes can be found at larger distances from the center of the lattice. For different values of the parameter m , we have determined the fractal dimension of the rabid cluster—that is the cluster containing all rabid foxes—as a function of time. If r_{\max} is the radius of this cluster, its fractal dimension δ is defined by $N_R(t) = \pi r_{\max}^\delta$, where $N_R(t)$ is the number of rabid foxes in the cluster. Figure 6 shows that δ tends to a constant value as time increases. This limit value increases when m decreases since, as expected, the density of rabid foxes is higher for lower values of m . For d_ℓ respectively equal to 0.005, 0.01, and 0.015, the corresponding limit values are 1.27, 1.25, and 1.22.

Figures 7a-7f show how the cluster containing the infected and infectious foxes grows as a function of time. Infected and infectious foxes are essentially localized at the boundary of the cluster. This feature corresponds to the small subsequent outbreaks following the first one. This is also clearly illustrated in Figures 5.

As for the coupled-map lattice model, we have determined numerically how the speed of the epizootic wavefront varies with the carrying capacity and the diffusion. Our results are represented in Figures 8 and 9. The curves representing the variation of the speed of the epizootic wavefront as a function of d_ℓ show the existence of a threshold value, which, in particular, depends upon the parameter m .

4 Conclusion

We have investigated two different models of the spatial spread of rabies among foxes: a one-dimensional coupled-map lattice model, and a two-dimensional automata network model. In both models, the fox population is divided into three-species: susceptible, infected or incubating, and infectious or rabid. They are based on the fact that susceptible and incubating foxes are territorial while rabid foxes have lost their sense of direction and move erratically out of their territory propagating the disease. coupled-map lattice models and automata networks models have the advantage, compared to models formulated in terms of differential equations, to take into account the short-range character of the infection process. We have essentially studied how the spatial distribution of rabies,

and the speed of propagation of the epizootic front depend upon the carrying capacity or food availability of the environment and parameters characterizing the erratic motion of rabid foxes out of their territory. In agreement with ecological studies, our numerical simulations show that, decreasing food availability slows down the spread of the disease, and, that below a certain threshold, rabies eventually dies out. On the other hand increasing the parameters measuring the diffusive motion of rabid foxes favors the spread of the disease.

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Figure captions

Figure 1- Susceptible (S) and rabid (R) densities as functions of site location at time $t = 1800$ for $b = 0.01$, $d = 0.001$, $d_r = 0.1$, $p_1 = 0.8$, $p_r = 0.05$, $D = 0.1$, $d_\ell = 0.01$ (continuous line), and $d_\ell = 0.015$ (dashed line).

Figure 2- Fox populations densities as a function of site location at time $t = 1800$ for $b = 0.01$, $d = 0.001$, $d_\ell = 0.01$, $d_r = 0.1$, $p_1 = 0.8$, $p_r = 0.05$, $D = 0.1$ (dashed line), and $D = 0.2$ (continuous line).

Figure 3- Speed of the epizootic wavefront as a function of D for $b = 0.01$, $d = 0.001$, $d_r = 0.1$, $p_1 = 0.8$, $p_r = 0.05$, and two different values of d_ℓ indicated in the figure. These two set of data can be fitted with functions of the form $A\sqrt{D}$ (continuous lines)

Figure 4- Speed of the epizootic wavefront as a function of d_ℓ for $b = 0.01$, $d = 0.001$, $d_r = 0.1$, $p_1 = 0.8$, $p_r = 0.05$, and $D = 0.1$.

Figure 5- Fox populations densities as a function of site location at time $t = 1600$ for $b = 0.01$, $d = 0.001$, $d_r = 0.1$, $p_i = 0.8$, $p_r = 0.05$, and (a) $d_\ell = 0.01$, $m = 0.1$, (b) $d_\ell = 0.015$, $m = 0.1$, (c) $d_\ell = 0.015$, $m = 0.2$.

Figure 6- Fractal dimension of the rabid cluster as a function of time for $b = 0.01$, $d = 0.001$, $d_r = 0.1$, $p_i = 0.8$, $p_r = 0.05$, $m = 0.2$ and different values of d_ℓ indicated in the figure.

Figures 7- Spatial patterns obtained after different numbers of time steps. The symbols: \bullet , Δ , and $*$ denote, respectively, susceptible, infected and rabid foxes. Parameters values: $b = 0.01$, $d = 0.001$, $d_l = 0.001$, $d_r = 0.1$, $p_i = 0.8$, $p_r = 0.05$, $m = 0.2$. (a) $t = 0$, (b) $t = 50$ (c) $t = 100$, (d) $t = 200$, (e) $t = 500$, (f) $t = 800$.

Figure 8- Speed of the epizootic wavefront as a function of m for $b = 0.01$, $d = 0.001$, $d_r = 0.1$, $p_i = 0.8$, $p_r = 0.05$, and two different values of d_ℓ indicated in the figure.

Figure 9- Speed of the epizootic wavefront as a function of d_ℓ for $b = 0.01$, $d = 0.001$, $d_r = 0.1$, $p_i = 0.8$, $p_r = 0.05$, and two different values of m indicated in the figure.

























