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PROPAGATION OF SALMONELLA WITHIN AN INDUSTRIAL HEN HOUSE*

C. BEAUMONT†, J.-B. BURIE‡, A. DUCROT‡, AND P. ZONGO†

Abstract. We propose a mathematical spatial and age structured model to describe the spatial spread of *Salmonella* among laying hens in industrial hen houses. We provide a mathematical study of traveling pulses of infection and describe a minimal speed property for such a problem. The dependence with respect to some heterogeneities of the medium is also discussed. Finally, based on biological data, the parameters of the model are estimated to provide some information on the propagation speed of the bacteria.

Key words. population dynamics, epidemiology, age structured equation, traveling pulse, spreading speed, minimal speed

AMS subject classifications. 35K57, 35C07, 92D30

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1. Introduction.

1.1. Biological problem.

Salmonella is a major cause of food-borne illness in humans. Poultry products, mostly eggs and egg products, are most often the source of human contamination. *Salmonella enteritidis* is the strain which is most often found in such cases [13, 18]. Indeed, this bacterium may durably colonize the gastrointestinal tracks of fowls as well as their systemic organs such as spleen or liver; but, in most cases, it will not result in any visible clinical signs of disease which would help the farmer to identify contamination. This silent carrier-state will in turn lead to horizontal transmission within the flock after fecal shedding [28] or, for *Salmonella enteritidis*, into vertical transmission through the transovarian route [19]. *Salmonella* may be transmitted between animals or indirectly through contaminated environment (including water and feed; see, for example, [15, 28]). Many procedures exist to help prevent contamination by *Salmonella*, e.g., selection for increased animal genetic resistance [4] and vaccination [3, 50], but none of them results in zero risk.

In industrial hen houses, two housing system types are used: cages or floor rearing. In the cage systems, the population of hens is confined to cages that can contain up to fifty hens. The cages are aligned in separate rows allowing the farmer access to the animals (see the example in Figure 1.1). With floor rearing, the flock of hens is equally distributed within the hen house.

A number of field studies published in the last five years in the European Union have evaluated the effects of different housing systems on the *Salmonella* risk in laying hen flocks. These studies showed a higher prevalence of *Salmonella* in flocks housed in conventional cages compared with those reared on floor [25, 29, 46]. However, previous studies have detected a lower incidence of *Salmonella* in conventional cage

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†INRA, UR83 Recherches avicoles, F-37380 Nouzilly, France (Catherine.Beaumont@tours.inra.fr, pascal.zongo@gmail.com). This study was achieved while the fourth author benefited from a post-doctoral scholarship cofunded by the EADGENE network of excellence and INRA.
‡UMR CNRS 5251 IMB, Université de Bordeaux, 3 ter Place de la Victoire, 33076 Bordeaux, France (Jean-Baptiste.Burie@u-bordeaux2.fr, arnaud.ducrot@u-bordeaux2.fr).

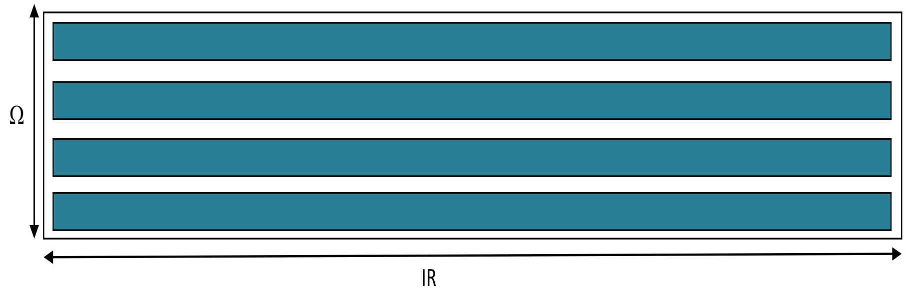


Fig. 1.1. *Schematic representation of a generic industrial hen house (top view) showing four rows of cages of hens (in gray) separated by free spaces allowing farmers to take care of the animals. For modeling, we assimilate the hen house to a cylindrical domain $\Sigma = \mathbb{R} \times \Omega$ where $\Omega \subset \mathbb{R}^d$.*

systems than cage-free systems [20, 26, 35]. These results are unclear and variable (see the overview of all observational studies in [45]) even between different cage systems.

1.2. Mathematical problem. Several models have already been proposed to study *Salmonella* spread within laying flocks [31, 32, 33, 51]; see also [42] and the references cited therein.

All of these models assume an indirect transmission of the disease through the bacteria density in the environment; see also [16, 17] for another example. In [31], a compartmental model based on a system of ODEs was considered: infected hens were structured with respect to the age of infection because transmission of bacteria from hens to eggs was assumed to depend on this variable.

This model was used in [33] to study the effect of genetic selection and vaccination on the disease propagation.

In [32], a spatial structure was added: the bacteria disperse via a diffusion process within the hen house, whereas the hen population is motionless since it is confined in cages. However, the total number of hens is assumed to be constant in time and uniform in space.

Recently, an individual-based model version of [32] including stochastic variability of the immune response of hens was proposed in [51] to take into account the host response to bacterial infection. Moreover, the hen population was not uniform in space but distributed in rows as in Figure 1.1. The outputs of this model will be used for calibration in our numerical experiments (section 7).

In this article, we introduce an extension of [31, 32] in which the hen distribution is not necessarily uniform, as in [51]. Moreover, we use a slightly more general modeling of the excretion rate of the bacteria by hens by taking into account the time elapsed since infection as a variable of the model.

We aim to understand the effect of different housing systems and, more generally, the effect of the heterogeneity of the hens' density on the epidemiology of *Salmonella* to suggest configurations that would keep the epizootic risk minimal.

As industrial hen houses are usually much longer than wide and as the diffusion of the bacteria is slow (see [51]), we model the hen house as a stripe denoted by $\Sigma = \mathbb{R} \times (0, L)$, where L is the width of the hen house, and we denote a point of Σ by (x, y), with $x \in \mathbb{R}$ and $y \in (0, L)$. However, our mathematical analysis is still valid if we consider a general cylindrical domain $\Sigma = \mathbb{R} \times \Omega$, where $\Omega \subset \mathbb{R}^d$, with $d \in \mathbb{N}^*$ some bounded open set with sufficiently smooth boundary.

TABLE 1.1
State variables of model (1.1).

$C(t,x,y)$	Density of bacteria in the environment at time t and position (x,y)
$S(t,x,y)$	Density of susceptible hens at time t and position (x,y)
$i(a,t,x,y)$	Density of infected hens with respect to infection age a at time t and position (x,y)

The model we will consider reads as follows:

$$
(1.1)\qquad
\begin{aligned}
&\frac{\partial S(t,x,y)}{\partial t} = -\sigma S(t,x,y)C(t,x,y),\\
&\frac{\partial i(t,a,x,y)}{\partial t} + \frac{\partial i(t,a,x,y)}{\partial a} = 0,\\
&i(t,0,x,y) = \sigma S(t,x,y)C(t,x,y),\\
&\frac{\partial C(t,x,y)}{\partial t} = D\Delta_{x,y}C(t,x,y) - \alpha C(t,x,y) + \int_0^\infty \beta(a)i(t,a,x,y)da,
\end{aligned}
$$

together with nonflux boundary conditions (reflecting the confinement of the populations in the domain):

$$
(1.2)\qquad \nabla C(t,x,y)\cdot \nu_\Sigma(x,y) = 0,\ \ (t,x,y)\in(0,\infty)\times\mathbb{R}\times\partial\Omega.
$$

Here $t>0$ while $(x,y)\in\mathbb{R}\times\Omega$, and $\nu_\Sigma(x,y)$ denotes the outward unit normal vector of Σ at $(x,y)\in\mathbb{R}\times\partial\Omega$. This model is supplemented with initial data

$$
(1.3)\qquad S(0,x,y) = S_0(x,y),\ \ i(0,a,x,y) = i_0(a,x,y),\ \ C(0,x,y) = C_0(x,y),
$$

with $S_0\in L^\infty_+(\Sigma)$, $i_0\in L^1\left(0,\infty;L^\infty_+(\Sigma)\right)$, and $C_0\in C_{b+}\left(\overline{\Sigma}\right)$. Here $C_b\left(\overline{\Sigma}\right)$ denotes the Banach space of bounded and continuous functions on $\overline{\Sigma}$ endowed with the usual supremum norm, while $C_{b+}\left(\overline{\Sigma}\right)$ denotes its positive cone, consisting of the everywhere positive functions.

The density of bacteria in the environment at time $t\geq 0$ located at a position (x,y) is denoted by $C(t,x,y)$. Let $S(t,x,y)$ be the density of susceptible hens (those capable of contracting the disease) at time t and position (x,y). Now let $i(t,a,x,y)$ be the density of hens infected at time t with respect to age of infection a (more precisely, a is the elapsed time since infection) and position (x,y). The term $\beta(a)i(t,a,x,y)$ represents the density of bacteria excreted by hens infected with respect to the age of their infection a at time t and position (x,y). The flux of excreted bacteria at time t and position (x,y) is modeled by the expression $\int_0^\infty \beta(a)i(t,a,x,y)da$, while the flux of newly infected hens corresponds to the boundary condition for i at age $a=0$, namely, the third equation in (1.1). Furthermore, in the above system, σ denotes the transmission rate, α denotes the mortality rate of the bacteria, and D is the diffusion coefficient for their dispersal in the environment.

Our goal is to study the ability of a spatially localized initial infection to propagate into the susceptible population. In what follows, we shall focus on the situation when the initial distribution of susceptible hens, namely, $S_0\equiv S_0(x,y)$, will depend only on $y\in\Omega$. This assumption means that hens are homogeneously distributed over the length of the cylindrical domain Σ and spatial heterogeneities are due to the row structure (or stripped structure) in the repartition of hens only (see Figure 1.1).

We will discuss the propagation phenomenon for (1.1)–(1.3) with respect to the so-called basic reproduction number (denoted by R_0 in what follows). When propagation of infection takes place (namely, when $R_0 > 1$), we will show that the infection persists and spreads into the spatial domain with an asymptotic speed of spread (also called spreading speed) c^* together with an asymptotic pulse shape. This spreading speed of infection is then determined, and it will be shown that system (1.1) is linearly determinate, which means that the spreading speed can be determined from the linear equation obtained by linearizing around the zero state. Moreover, we prove that the asymptotic speed of spread coincides with the minimal speed of traveling waves for (1.1). (We refer the reader to van den Bosch, Metz, and Diekmann [44], Mollison [27], or Weinberger, Lewis, and Li [49] for some discussions and results on the linear conjecture in various contexts.)

The derivation of the above-mentioned results will be obtained by using ideas similar to those developed in [9, 10] and [37] (see also [34] and [40]; we also refer the reader to Britton [7]). If we introduce the auxiliary function $U \equiv U(t,x,y)$ defined by

$$U(t,x,y) = \sigma \int_0^t C(s,x,y)ds = \ln \frac{S_0(x,y)}{S(t,x,y)},$$

it satisfies the nonlocal parabolic equation

(1.4)
$$\begin{aligned}
&(\partial_t - \Delta_{x,y} + \alpha)\, U(t,x,y) = \sigma \int_0^t \beta(a) S_0(x,y) \left(1 - e^{-U(t-a,x,y)}\right) da + u_0(t,x,y),\\
&\nabla_y U(t,x,y) \cdot \nu_\Omega(y) = 0, \quad t > 0,\ x \in \mathbb{R},\ y \in \partial\Omega,\\
&U(0,x,y) \equiv 0,
\end{aligned}$$

wherein u_0 is a given function depending on the initial data for the infective components. Note that function U represents the local (spatial) history of the bacterial density. A mathematical study of the spreading properties of such an equation will provide information on the original system of (1.1)–(1.3).

The study of asymptotic speed of spread for reaction-diffusion equations has a long history (we refer the reader to the works of Aronson and Weinberger [1, 2]). It has been extended in various contexts and applications. See, for instance, the works of Diekmann [8, 10] and Thieme [38, 39] for research on the asymptotic speed of spread for scalar integral equations. Many extensions have been provided during the last decade, including the study of integral equations without monotonicity assumption (see [14, 41] and the references therein), systems of integral equations (see [34]), time-delay reaction-diffusion equations (see, for instance, [21] and the references therein), and spatially periodic (and also more general) environments (see, for instance, [5, 22, 48] and the references therein).

However, none of the above-mentioned results exactly applies to (1.4) because of the geometry of the problem (spatial heterogeneity on the section Ω).

We will first derive some results for the auxiliary variable U. This will be used to obtain information on the original variables of system (1.1)–(1.3). Finally qualitative properties of the spreading speed with respect to the dispersal of the bacteria and to the heterogeneity of the spatial distribution (row structure) of the hens will be studied in order to derive some biological hints to eradicate or at least slow down the propagation of the disease.

The paper is organized as follows: In section 2 we present the main mathematical results of this work. Section 3 is concerned with preliminary results including well-posedness of (1.1)–(1.3), definition of traveling waves, and basic properties of some characteristic equation. Section 4 is devoted to the study of the asymptotic speed of spread, while section 5 deals with existence of traveling wave solutions. The influence of the heterogeneities is studied in section 6, followed by numerical experiments in section 7 and concluding remarks in section 8.

2. Main results.

In this section, we will give an exposition of the main results of this work. First of all, we will normalize the diffusion coefficient D to 1 by using a simple rescaling argument $(x, y) = \frac{1}{\sqrt{D}}(x, y)$. Thus, throughout this work, we will always assume that $D = 1$.

These results are related to dynamical properties of system (1.1)–(1.2) together with (1.3). Let us introduce for each function $\gamma \in L^\infty(\Omega)$ the principal eigenvalue $\Lambda(\gamma) \in \mathbb{R}$ of the following elliptic problem:

$$\begin{aligned} &\Delta\psi + \gamma(y)\psi = \Lambda(\gamma)\psi \text{ in } \Omega, \\ &\nabla\psi(y) \cdot \nu_\Omega(y) = 0 \text{ for each } y \in \partial\Omega, \\ &\psi(y) > 0 \text{ for each } y \in \overline{\Omega}, \end{aligned} \tag{2.1}$$

wherein the vector $\nu_\Omega(y)$ denotes the outward normal unit vector of Ω at $y \in \partial\Omega$.

Next, we make an assumption concerning the age distribution of the bacteria excretion rate of hens.

ASSUMPTION 2.1. *We assume that*

$$\beta \in L^1_+(0, \infty) \cap L^\infty_+(0, \infty).$$

We also make an assumption on the initial data.

ASSUMPTION 2.2. *We assume that $S_0(x, y) \equiv S_0(y)$ with $S_0 \in L^\infty_+(\Omega)$, $C_0 \in C_{b+}(\overline{\Sigma})$, while $i_0 \in L^1\left(0, \infty; L^\infty(\overline{\Sigma})\right)$. Here $C_b(\overline{\Sigma})$ denotes the space of continuous and bounded functions from $\overline{\Sigma}$ into $\mathbb{R}$, while $C_{b+}(\overline{\Sigma})$ denotes its positive cone.*

We furthermore assume that the infective initial data are spatially localized; namely, the function $\widehat{u} := \widehat{u}(x, y) = C_0(x, y) + \|\beta\|_{L^1(0,\infty)}\|i_0(\cdot, x, y)\|_{L^1(0,\infty)}$ is a nonzero, positive, continuous function over $\overline{\Sigma}$ and with a compact support.

With Assumptions 2.1 and 2.2, we set

$$R_0 = \frac{1}{\alpha}\Lambda\left(\sigma\int_0^\infty \beta(l)dl\ S_0(\cdot)\right). \tag{2.2}$$

As will be seen latter, the above parameter will play the role of an epidemic threshold. If one forgets the spatial heterogeneity by setting $S_0(y) \equiv S_0 > 0$ for the moment, R_0 reads as follows:

$$R_0 = \sigma S_0 \times \frac{1}{\alpha} \times \int_0^\infty \beta(a)da. \tag{2.3}$$

In such a case, the first term in (2.3) describes the number of susceptible hens infected by unit of time and bacteria. This is weighted by the average lifetime of a bacterium. Finally the last term represents the number of new bacteria produced by these infected hens during their infectious period. Hence, in the spatially homogeneous setting, R_0 describes the number of bacteria produced by a single bacteria introduced in the infection-free environment.

We will now describe the different behaviors of the system with respect to the value of R_0 (see (2.2)). Our first result shows that when $R_0 \leq 1$ then the infection cannot persist into the population and does not spread.

THEOREM 2.3. *Let Assumptions* 2.1 *and* 2.2 *be satisfied. If* $R_0 \leq 1$, *then the solution* (S, i, C) *of* (1.1) *with initial data* (S_0, i_0, C_0) *satisfies*

$$\lim_{t\to\infty} \sup_{(x,y)\in\overline{\Sigma}} C(t,x,y) = 0,$$
$$\lim_{t\to\infty} \sup_{(x,y)\in\overline{\Sigma}} i(t,0,x,y) = 0,$$

and for each function $\varepsilon : (0,\infty) \to [0,\infty)$ *such that* $\varepsilon(t) \to \infty$ *as* $t \to \infty$, *one has*

$$\lim_{t\to\infty} \sup_{|x|\geq\varepsilon(t),\ y\in\Omega} |S_0(y) - S(t,x,y)| = 0.$$

When $R_0 > 1$, let us now define the quantity $\Gamma \in (0,\infty)$ by

$$\Gamma = \sup_{x>0} \frac{1}{x^2} \left\{ x + \alpha - \Lambda\left(\sigma \int_0^\infty \beta(l) e^{-lx} dl\ S_0(\cdot)\right)\right\}, \tag{2.4}$$

where Λ is defined in (2.1), and c^* by

$$c^* = \frac{1}{\sqrt{\Gamma}}. \tag{2.5}$$

The above quantities will allow us to describe some dynamical properties of the propagation of the epizootic.

THEOREM 2.4 (asymptotic pulse shape of infection). *Let Assumptions* 2.1 *and* 2.2 *be satisfied. If* $R_0 > 1$, *then the epizootic persists, in the sense that*

$$\liminf_{t\to\infty} \sup_{(x,y)\in\overline{\Sigma}} C(t,x,y) > 0, \tag{2.6}$$

and there exists $\delta > 0$ *such that for each* $\varphi \in L^1_+(\Omega)$

$$\liminf_{t\to\infty} \sup_{x\in\mathbb{R}} \int_\Omega \varphi(y) i(t,0,x,y) dy \geq \delta \int_\Omega \varphi(y) S_0(y) dy. \tag{2.7}$$

Furthermore, (1.1)–(1.3) *has the following spreading speed property:*

(i) *For each* $c > c^*$, *one has*

$$\lim_{t\to\infty} \sup_{|x|\geq ct,\ y\in\Omega} C(t,x,y) = 0, \quad \lim_{t\to\infty} \sup_{|x|\geq ct,\ y\in\Omega} i(t,0,x,y) = 0.$$

(ii) *For each* $c \in (0, c^*)$, *one has*

$$\lim_{t\to\infty} \sup_{|x|\leq ct,\ y\in\Omega} C(t,x,y) = 0, \quad \lim_{t\to\infty} \sup_{|x|\leq ct,\ y\in\Omega} i(t,0,x,y) = 0.$$

Furthermore, the density of susceptible has an asymptotic traveling wave shape, in the following sense:

(iii) *For each* $c > c^*$, *one has*

$$\lim_{t\to\infty} \sup_{|x|\geq ct} \|S(t,x,\cdot) - S_0(\cdot)\|_{L^\infty(\Omega)} = 0.$$

(iv) *There exists $\eta > 0$ such that for each $c \in (0, c^*)$, one has*

$$\limsup_{t\to\infty} \sup_{|x|\le ct} S(t,x,y) \le S_0(y)e^{-\eta},$$

uniformly with respect to $y \in \Omega$.

The above result shows that the C-component as well as the density of newly infected animals (at age of infection zero) of the system propagate into the spatial domain with an asymptotic pulse shape and with asymptotic speed of spread c^*. However, we are not able to prove that the width of this pulse solution remains bounded with respect to time.

We furthermore expect that similarly to the classical Fisher-KPP equation, the motion of the level line exhibits a logarithmic phase (see, for instance, [6, 43] for the one-dimensional Fisher-KPP equation). In the context of (time distributed) nonlocal equations, such a result seems to be unknown. For reaction-diffusion equations with discrete time delay, one can obtain such a logarithmic phase as a consequence of precise estimates of the corresponding heat kernel derived in Theorem 2.3 in [24]. Such a step seems to be crucial in order to understand the approach to waves.

We now deal with the existence and nonexistence results of traveling solutions for system (1.1)–(1.3). A precise definition of such solutions will be given in the next section. It will be shown that the existence of wave solutions for (1.1)–(1.3) is equivalent to finding a speed $c > 0$ and a positive and bounded profile solution of the following nonlocal elliptic equation:

$$\begin{aligned}
&-\left(\Delta_{x,y} + c\partial_x - \alpha\right) u(x,y) = \frac{\sigma}{c} S_0(y) \int_x^\infty \beta\left(\frac{l-x}{c}\right) u(l,y) e^{-\frac{\sigma}{c}\int_l^\infty u(s,y)ds} dl,\\
&\nabla_y u(x,y)\cdot \nu_\Omega(y) = 0, \quad x\in\mathbb{R},\ y\in\partial\Omega,\\
&\lim_{x\to\pm\infty} u(x,y) = 0 \quad \forall y\in\Omega.
\end{aligned}$$

Note that it is related to a given and fixed function $S_0 \equiv S_0(y)$.

THEOREM 2.5. *Let $S_0 \in L_+^\infty(\Omega)$ be given. Let Assumption* 2.1 *be satisfied. If $R_0 \le 1$, then system* (1.1) *does not have any traveling wave solution.*

Our next result is concerned with the existence of traveling waves.

THEOREM 2.6 (existence). *Let $S_0 \in L_+^\infty(\Omega)$ be given. Let Assumption* 2.1 *be satisfied. Recalling* (2.2)*, we assume that $R_0 > 1$. Then, for each $c \ge c^*$, system* (1.1) *has a traveling wave solution with the wave speed c.*

Our next result deals with a nonexistence result for sufficiently small wave speeds.

THEOREM 2.7 (minimal wave speed). *Let $S_0 \in L_+^\infty(\Omega)$ be given. Let Assumption* 2.1 *be satisfied. If $R_0 > 1$, then system* (1.1) *does have a traveling wave solution for all wave speeds $c \in (0, c^*)$, where c^* is defined in* (2.5).

In the above-mentioned results, one may observe that R_0 provides an epidemic threshold but also that c^* is the minimal wave speed of the system. Due to Theorem 2.4, the minimal wave speed coincides with the spreading speed of the disease for spatially localized infective initial data.

We now aim to understand the influence of the heterogeneity of the function S_0 on the minimal speed of propagation. For such a study, we will assume that Ω is a one-dimensional interval $(0, L)$ so that $\Sigma = \mathbb{R} \times (0, L)$ becomes a two-dimensional strip. Next for each $N_0 > 0$, we consider the set

$$\mathcal{A}(N_0) = \left\{ S_0 \in L_+^\infty(0,L) : \ \frac{1}{L}\int_0^L S_0(y)dy = N_0 \right\},$$

and we explicitly write down the dependence of R_0, Γ, and c^* with respect to S_0.

THEOREM 2.8. *Let Assumption* 2.1 *be satisfied. For each* $N_0 > 0$*, we have*

$$\inf_{S_0 \in \mathcal{A}(N_0)} R_0(S_0) = R_0(N_0) = \frac{\sigma N_0}{\alpha} \int_0^\infty \beta(l) dl.$$

Moreover if

$$\frac{\sigma N_0}{\alpha} \int_0^\infty \beta(l) dl > 1,$$

then

$$\inf_{S_0 \in \mathcal{A}(N_0)} c^*(S_0) = c^*(N_0).$$

This result means that the minimum wave speed observed for a spatially heterogeneous distribution of hens is always larger than the minimum wave speed observed for the corresponding averaged spatially homogeneous one.

According to the value of the biological parameters (see section 7), it is relevant to look at the slow diffusion asymptotic $D \to 0$. Due to the rescaling argument explained at the beginning of this section, when dealing with $\Omega = (0, L)$, this slow diffusion asymptotic corresponds to the asymptotic $L \to \infty$. We make the following assumption.

ASSUMPTION 2.9. *We assume that* $\Omega = \Omega_L = (0, L)$ *for some* $L > 0$*, and we consider* $S_0 \equiv S_L$ *defined by*

$$S_L(y) = \widetilde{S}_0\left(\frac{y}{L}\right),$$

where $\widetilde{S}_0 \in L^\infty_+(0, 1)$ *is fixed.*

We derive the asymptotic behavior of $R_0 = R_0(L)$ as well as the corresponding minimal wave speed $c^* = c^*(L)$ with respect to L when $L \to \infty$.

THEOREM 2.10 (slow diffusion asymptotic). *Let Assumption* 2.9 *be satisfied. Then the map* $L \mapsto R_0(L)$ *is increasing and we have*

$$\lim_{L \to \infty} R_0(L) = R_0^\infty := \frac{\sigma \|\widetilde{S}_0\|_\infty}{\alpha} \int_0^\infty \beta(l) dl. \tag{2.8}$$

If $R_0^\infty > 1$*, then* $c^*(L)$ *is well defined for large enough values of* L*, the map* $L \mapsto c^*(L)$ *is increasing, and we have*

$$\lim_{L \to \infty} c^*(L) = \frac{1}{\sqrt{\Gamma_\infty}},$$

wherein we have set

$$\Gamma_\infty = \sup_{x > 0} \frac{1}{x^2} \left\{ x + \alpha - \sigma \|\widetilde{S}_0\|_\infty \int_0^\infty \beta(l) e^{-lx} dl \right\}.$$

This result proves that the minimum wave speed observed for the heterogeneous distribution of hens is close to the one for the homogeneous one, where the constant hen density is equal to the maximum density of the heterogeneous distribution.

3. Preliminaries.

3.1. Weak solution of system (1.1)–(1.3). The aim of this section is to consider system (1.1)–(1.3). We will prove the existence and uniqueness of suitable weak solutions and give various reformulations of this problem in terms of a scalar nonlocal parabolic equation or scalar integral equation for which comparison arguments can be applied. Let us assume that $S_0 \equiv S_0(x,y) \in L^\infty_+(\Sigma)$, $C_0 \in C_{b+}(\overline{\Sigma})$, and $i_0 \in L^1\left(0,\infty; L^\infty(\overline{\Sigma})\right)$. Then let us first notice that the second equation in (1.1) can be integrated along the characteristic to lead us to

$$i(t,a,x,y) = \begin{cases} i(t-a,0,x,y) \text{ if } t > a \geq 0, \\ i_0(a-t,x,y) \text{ if } 0 \leq t < a, \end{cases} \tag{3.1}$$

so that the boundary condition at $a = 0$ allows us to reduce the system to the following problem:

$$\begin{cases} S(t,x,y) = S_0(x,y) e^{-\sigma \int_0^t C(s,x,y)ds}, \\ \frac{\partial C(t,x,y)}{\partial t} = \Delta_{x,y} C(t,x,y) - \alpha C(t,x,y) + \int_0^\infty \beta(a) i(t,a,x,y)da, \\ \nabla C(t,x,y) \cdot \nu_\Sigma(x,y) = 0, \quad (t,x,y) \in (0,\infty) \times \mathbb{R} \times \partial\Omega, \end{cases} \tag{3.2}$$

with

$$i(t,a,x,y) = \begin{cases} \sigma S(t-a,x,y) C(t-a,x,y) \text{ if } t > a \geq 0, \\ i_0(a-t,x,y) \text{ if } 0 \leq t < a. \end{cases} \tag{3.3}$$

This allows us to reduce the problem to the following scalar equation for C:

$$\begin{aligned} (\partial_t - \Delta_{x,y} + \alpha)\, C(t,x,y) &= \int_0^t \beta(a) \sigma S_0(x,y) C(t-a,x,y) e^{-\sigma \int_0^{t-a} C(s,x,y)ds} da \\ &\quad + \int_t^\infty \beta(a) i_0(a-t,x,y) da, \\ \nabla C(t,x,y) \cdot \nu_\Sigma(x,y) &= 0 \text{ for } (t,x,y) \in (0,\infty) \times \mathbb{R} \times \partial\Omega, \\ C(0,x,y) &= C_0(x,y) \text{ for } (x,y) \in \overline{\Sigma}. \end{aligned} \tag{3.4}$$

This reformulation allows us to provide the following definition of a weak solution for system (1.1)–(1.3).

DEFINITION 3.1. *Let $S_0 \in L^\infty_+(\Sigma)$, $C_0 \in C_{b+}(\overline{\Sigma})$, and $i_0 \in L^1\left(0,\infty; L^\infty_+(\overline{\Sigma})\right)$ be given. The 3-uplet (S,i,C) is said to be a weak solution of* (1.1)–(1.3) *on* $[0,T]$ *if*

(i) *function $C \in C^0\left([0,T] \times \overline{\Sigma}\right) \cap W^{1,2}_{p,loc}\left((0,T) \times \Sigma\right)$ for each $p \in (1,\infty)$ and satisfies* (3.4) *for almost all $(t,x,y) \in (0,T) \times \Sigma$;*

(ii) *function S satisfies*

$$S(t,x,y) = S_0(x,y) e^{-\sigma \int_0^t C(s,x,y)ds},$$

while i satisfies (3.3).

We will now look for an equivalent formulation of the weak solution of (1.1)–(1.3). Let (S,i,C) be a weak solution of (1.1)–(1.3) on $[0,T]$. According to the above definition, function C satisfies

$$\begin{aligned} (\partial_t - \Delta_{x,y} + \alpha)\, C(t,x,y) &= \frac{\partial}{\partial t} \int_0^t \beta(a) S_0(x,y) \left(1 - e^{-\sigma \int_0^{t-a} C(s,x,y)ds}\right) da \\ &\quad + \int_t^\infty \sigma \beta(a) i_0(a-t,x,y) da, \\ \nabla C(t,x,y) \cdot \nu_\Sigma(x,y) &= 0, \quad (t,x,y) \in (0,\infty) \times \mathbb{R} \times \partial\Omega, \end{aligned}$$

together with the initial data $C(0,x,y)=C_0(x,y)$. As a consequence, setting

$$U(t,x,y)=\sigma\int_0^t C(s,x,y)ds$$

leads us to the equation

(3.5)
$$\begin{aligned}&(\partial_t-\Delta_{x,y}+\alpha)\,U(t,x,y)=\sigma\int_0^t\beta(a)S_0(x,y)\left(1-e^{-U(t-a,x,y)}\right)da+u_0(t,x,y),\\&\nabla_y U(t,x,y)\cdot\nu_\Omega(y)=0,\ \ t>0,\ x\in\mathbb{R},\ y\in\partial\Omega,\\&U(0,x,y)\equiv 0,\end{aligned}$$

wherein we have set

$$u_0(t,x,y)=\sigma\left(C_0(x,y)+\int_0^t\int_s^\infty\beta(a)i_0(a-s,x,y)dads\right), \tag{3.6}$$

and where $U\in W^{1,2}_{p,loc}\left((0,T)\times\Sigma\right)$ for each $p\in(1,\infty)$ is increasing with respect to time t and $C=\frac{1}{\sigma}\partial_t U$ also belongs to $W^{1,2}_{p,loc}\left((0,T)\times\Sigma\right)$ for each $p\in(1,\infty)$.

Then the following lemma holds true.

Lemma 3.2. *Assume that $S_0\in L^\infty_+(\Sigma)$, $C_0\in C_{b+}(\overline{\Sigma})$, and $i_0\in L^1\left(0,\infty;L^\infty_+(\overline{\Sigma})\right)$. Then system (3.5)–(3.6) has a unique positive and globally defined solution $U\in C^0\left([0,\infty)\times\overline{\Sigma}\right)$ such that*

$$\begin{aligned}&U(t,x,y)\le M\left(S_0,C_0,i_0\right)\ \forall(t,x,y)\in[0,\infty)\times\overline{\Sigma},\\&\text{with } M\left(S_0,C_0,i_0\right):=\frac{\sigma}{\alpha}\left(\|S_0\|_\infty\|\beta\|_{L^1}+\|C_0\|_\infty+\|\beta\|_{L^1}\|i_0\|_{L^1(L^\infty)}\right),\end{aligned}$$

and for each $p\in(1,\infty)$, we have $U\in W^{1,2}_{p,loc}\left((0,\infty)\times\Sigma\right)$ and (3.5) is satisfied almost everywhere. Furthermore, for each $p\in(1,\infty)$, $\partial_t U\in W^{1,2}_{p,loc}\left((0,\infty)\times\Sigma\right)$, $\partial_t U\ge 0$, and the function $C:=\frac{1}{\sigma}\partial_t U$ satisfies (3.4) almost everywhere. In addition, C is uniformly bounded. More specifically, one has

$$C(t,x,y)\le e^{-\alpha t}\|C_0\|_\infty+\frac{\|\beta\|_\infty}{\alpha}\left(\|S_0\|_\infty M\left(S_0,C_0,i_0\right)+\sigma\|i_0\|_{L^1(L^\infty)}\right).$$

The above lemma therefore proves the existence and uniqueness of a globally defined weak solution of (1.1)–(1.3). It also provides the expression of the solution in terms of U, the solution of (3.5), as well as a uniform estimate of the C-component of (1.1)–(1.3). This reformulation will be extensively used in what follows to prove the results mentioned in the previous section. Note that the comparison principle can be applied to (3.5).

3.2. Traveling wave formulation. The aim of this section is to deal with a traveling wave solution for (1.1). To achieve it, let us first give the definition of a complete orbit for (1.1).

Definition 3.3 (entire weak solution). *We will say that the 3-uplet (S,i,C) with $S:\mathbb{R}\times\Sigma\to\mathbb{R}^+$, $i:\mathbb{R}\times(0,\infty)\times\Sigma\to\mathbb{R}^+$, and $C:\mathbb{R}\times\overline{\Sigma}\to\mathbb{R}^+$ is an entire weak solution of (1.1)–(1.2) if for each $s\in\mathbb{R}$, one has*

(i) *$S(s,\cdot)\in L^\infty_+(\Sigma)$, $i(s,\cdot,\cdot)\in L^1\left(0,\infty;L^\infty_+(\Sigma)\right)$ and $C(s,\cdot)\in C_{b+}\left(\overline{\Sigma}\right)$;*

(ii) $(S(s+\cdot,\cdot), i(s+\cdot,\cdot,\cdot), C(s+\cdot,\cdot)$ *is a weak solution of* (1.1) *on* $[0,\infty)$ *with initial data* $(S(s,\cdot), i(s,\cdot,\cdot), C(s,\cdot))$.

We are now able to deal with the definition of a traveling wave for (1.1).

A traveling wave solution with speed $c > 0$ for system (1.1) is an entire weak solution with a constant profile and moving in space in the x-direction at the constant speed c. It consists in looking at special solutions of the form

$$S(t,x,y) = w(x-ct,y), \quad i(t,a,x,y) = v(a,x-ct,y), \quad C(t,x,y) = u(x-ct,y). \tag{3.7}$$

Since we are interested in propagation of epizootics, we will impose that ahead of the infective front, the density of susceptible is not yet affected by the epizootic so that

$$w(\infty,y) \equiv S_0(y),$$

where $S_0 \in L^\infty_+(\Omega)$ is a given heterogeneity on the section Ω of the cylinder Σ. Therefore, we will impose the following behavior on the solutions:

$$\begin{aligned} &\lim_{\xi\to\infty} (w(\xi,y), v(a,\xi,y), u(\xi,y)) = (S_0(y),0,0) \ \text{ almost everywhere,} \\ &\lim_{\xi\to-\infty} (v(a,\xi,y), u(\xi,y)) = (0,0) \ \text{ almost everywhere.} \end{aligned} \tag{3.8}$$

Ahead of the front ($x \to \infty$), the environment is not affected by the disease yet. However, behind the front ($x \to -\infty$), the population of susceptible hens has been affected and $w(-\infty,y)$ is unknown (the density of susceptible hens after the epizootics) and the infected component has a pulse-like shape.

As will be developed later in this section, one will have the following result.

LEMMA 3.4. *A profile* (w,v,u) *is a wave solution with speed* $c>0$ *of* (1.1) *with conditions* (3.8) *if and only if*

(i) *function* u *satisfies*

$$\begin{aligned} &-(\Delta_{x,y} + c\partial_x - \alpha)\, u(x,y) = \frac{\sigma}{c} S_0(y) \int_x^\infty \beta\left(\frac{l-x}{c}\right) u(l,y) e^{-\frac{\sigma}{c}\int_l^\infty u(s,y)ds} dl, \\ &\nabla_y u(x,y)\cdot \nu_\Omega(y) = 0, \ \ x\in\mathbb{R}, \ y\in\partial\Omega, \\ &\lim_{x\to\pm\infty} u(x,y) = 0 \ \ \forall y\in\Omega; \end{aligned} \tag{3.9}$$

(ii) *functions* w *and* v *satisfy*

$$w(x,y) = S_0(y) e^{-\int_x^\infty u(l,y)dl}, \quad v(a,x,y) = \sigma u(x+ca,y) w(x+ca,y).$$

Proof. Note that from the definition of entire weak solutions, for each $s\in\mathbb{R}$ and $t\ge 0$, function i satisfies

$$i(t+s,a,x,y) = i(t+s-a,0,x,y) \text{ if } t>a>0.$$

Due to the definition of traveling waves, $i(t,a,x,y) = v(a,x-ct,y)$, and hence for each $s\in\mathbb{R}$,

$$v(a-c(t+s),x,y) = v(0,x-c(t-a+s),y) \text{ if } t>a>0.$$

Setting $s=-t$, we deduce that there exists a function V such that

$$v(a,x,y) = v(0,x+ca,y) := V(x+ca,y).$$

As a consequence, one obtains that traveling wave solutions are special entire solutions of (1.1) of the form

$$S(t,x,y)=w(x-ct,y),\ \ i(t,a,x,y)=V(x-c(t-a),y),\ \ C(t,x,y)=u(x-ct,y).$$

Moreover, for each $t\in\mathbb{R}$ and $s\geq 0$, one has

$$w(x-c(t+s),y)=w(x-ct,y)e^{-\sigma\int_t^{t+s}u(x-cl,y)dl}=w(x-ct,y)e^{-\sigma\int_0^s u(x-ct-cl,y)dl}.$$

Setting $\xi=x-ct$ yields

$$w(\xi-cs,y)=w(\xi,y)e^{-\sigma\int_0^s u(\xi-cl,y)dl}=w(\xi,y)e^{-\frac{\sigma}{c}\int_{\xi-cs}^{\xi}u(l,y)dl},$$

so that

$$w(\xi,y)=w(\xi+cs,y)e^{-\frac{\sigma}{c}\int_{\xi}^{\xi+cs}u(l,y)dl},$$

and due to (3.8), letting $s\to-\infty$ leads us to

$$w(\xi,y)=S_0(y)e^{-\frac{\sigma}{c}\int_{\xi}^{\infty}u(l,y)dl}.$$

Similarly

$$V(\xi,y)=\sigma w(\xi,y)u(\xi,y)$$

and

$$\left(\Delta_{\xi,y}+c\partial_\xi-\alpha\right)u(\xi,y)+\int_0^\infty\sigma\beta(a)w(\xi+ca,y)u(\xi+ca,y)da=0.$$

As a consequence of the above algebra, if (w,v,u) is a traveling wave of (1.1) together with (3.8), one obtains that

$$v(a,x,y)=V(x+ca,y),\ \text{with}\ \ \forall x\in\mathbb{R},\ \int_x^\infty V(l,y)dl<\infty\ \text{almost everywhere},$$

and

$$w(x,y)=S_0(y)e^{-\frac{\sigma}{c}\int_x^\infty u(l,y)dl},$$

and finally

$$\begin{cases}-\left(\Delta_{x,y}+c\partial_x-\alpha\right)u(x,y)=\frac{\sigma}{c}S_0(y)\int_x^\infty\beta\left(\frac{l-x}{c}\right)u(l,y)e^{-\frac{\sigma}{c}\int_l^\infty u(s,y)ds}dl,\\ \nabla_y u(x,y)\cdot\nu_\Omega(y)=0,\ \ x\in\mathbb{R},\ y\in\partial\Omega,\\ \lim_{x\to\pm\infty}u(x,y)=0\ \ \forall y\in\Omega.\end{cases}$$

Conversely, let $u:\overline{\Sigma}\to\mathbb{R}^+$ be a positive and bounded solution of (3.9) for some given $c>0$. Assume furthermore that $u\in L^1\left((0,\infty)\times\Omega\right)$. Next, setting

$$w(x,y)=S_0(y)e^{-\int_x^\infty u(l,y)dl},\ \ V(\xi,y)=\sigma u(\xi,y)w(\xi,y),$$

one gets that (3.8) holds true. Setting

$$S(t,x,y)=w(x-ct,y),\ \ i(t,a,x,y)=V(x+ca-ct,y),\ \ C(t,x)=u(x-ct,y),$$

one easily obtains that (S,i,C) is an entire weak solution of (1.1). $\square$

Let us first derive some initial qualitative properties of the wave solutions.

LEMMA 3.5. *Let $c > 0$ be given. Let u be a positive bounded solution of* (3.9). *Then $u \in C\left(\overline{\Sigma}\right)$, and for each $y \in \overline{\Omega}$ one has*

$$u(\cdot, y) \in L^1(\mathbb{R}),$$

and function $U(y) := \frac{\sigma}{c}\int_{\mathbb{R}} u(x,y)dy$ satisfies

$$\begin{aligned}
&-\Delta U(y) + \alpha U(y) = \sigma S_0(y)\int_0^\infty \beta(a)\,da\left(1 - e^{-U(y)}\right),\\
&\nabla_y U(y)\cdot \nu_\Omega(y) = 0 \ \ \forall y \in \partial\Omega.
\end{aligned}$$

Proof. First note that the map $(x,y) \to S_0(y)\int_x^\infty \beta\left(\frac{l-x}{c}\right)u(l,y)e^{-\int_l^\infty u(s,y)ds}dl$ is bounded on Σ, and therefore elliptic regularity implies that $u \in W^{2,p}_{loc}(\Sigma)$. As a consequence, the convergence $\lim_{x\to\pm\infty} u(x,y) = 0$ for each $y \in \Omega$ holds true for the topology of $C^1\left(\overline{\Omega}\right)$. For each $M > 0$, consider $U_M \in C\left(\overline{\Omega}\right)$ defined by

$$U_M(y) = \int_{-M}^{M} u(x,y)dx.$$

It satisfies

$$\begin{aligned}
&-\left(u_x(M,y) - u_x(-M,y) + cu(M,y) - cu(-M,y)\right) - \Delta U_M(y) + \alpha U_M(y)\\
&= \frac{\sigma}{c}S_0(y)\int_{-M}^{M}\int_x^\infty \beta\left(\frac{l-x}{c}\right)u(l,y)e^{-\frac{\sigma}{c}\int_l^\infty u(s,y)ds}dl.
\end{aligned}$$

Consider the set $A \subset \overline{\Omega}$ defined by

$$A = \left\{y \in \overline{\Omega} : \ \int_0^\infty u(l,y)dy < \infty\right\}.$$

Note that for each $y \in A$, one has

$$\int_x^\infty \frac{\sigma}{c}\beta\left(\frac{l-x}{c}\right)u(l,y)e^{-\frac{\sigma}{c}\int_l^\infty u(s,y)ds}dl = \partial_x\int_0^\infty \beta\left(\frac{a}{c}\right)\left(1 - e^{-\frac{\sigma}{c}\int_{a-x}^\infty u(s,y)ds}\right)da,$$

while for all $y \in \overline{\Omega}\setminus A$,

$$\int_x^\infty \sigma\beta\left(\frac{l-x}{c}\right)u(l,y)e^{-\int_l^\infty u(s,y)ds}dl = 0.$$

Therefore one gets

$$\begin{aligned}
&-\left(u_x(M,y) - u_x(-M,y) + cu(M,y) - cu(-M,y)\right) - \Delta U_M(y)\alpha U_M(y)\\
&= S_0(y)\int_0^\infty \beta\left(\frac{a}{c}\right)\left(e^{-\frac{\sigma}{c}\int_{a+M}^\infty u(s,y)ds} - e^{-\frac{\sigma}{c}\int_{a-M}^\infty u(s,y)ds}\right)da,\\
&\nabla_y U_M(y)\cdot\nu_\Omega(y) = 0 \ \ \forall y \in \partial\Omega.
\end{aligned}$$

Letting $M \to \infty$ and using the Lebesgue convergence theorem leads us to elliptic estimates, and the family $\{U_M\}$ is bounded in $W^{2,p}(\Omega)$ for each $p \in (1,\infty)$. As a consequence, there exists a sequence $\{M_n\}_{n\geq 0}$ tending to ∞ as $n \to \infty$ such that

$$U_{M_n}(y) \to V(y) := \int_{\mathbb{R}} u(x,y)dy \text{ for the topology of } C^1\left(\overline{\Omega}\right).$$

Furthermore, letting $n \to \infty$ into the above equation leads us to

$$-\Delta V(y) + \alpha V(y) = S_0(y) \int_0^\infty \beta\left(\frac{a}{c}\right) da \left(1 - e^{-\frac{\sigma}{c}V(y)}\right),$$
$$\nabla_y V(y) \cdot \nu_\Omega(y) = 0 \ \ \forall y \in \partial\Omega.$$

The result follows by setting $U = \frac{\sigma}{c} V$. ∎

This preliminary results allow us to prove Theorem 2.5. Indeed the following result classically holds true.

LEMMA 3.6. *Let Assumption* 2.1 *be satisfied. Then the elliptic logistic-type problem*

$$-\Delta U(y) + \alpha U(y) = \sigma S_0(y) \int_0^\infty \beta(a)\, da \left(1 - e^{-U(y)}\right),$$
$$\nabla_y U(y) \cdot \nu_\Omega(y) = 0 \ \ \forall y \in \partial\Omega$$

has a nontrivial solution denoted by $U^* \equiv U^*(y)$ if and only if $R_0 > 1$. Furthermore, when it exists, it is unique.

As seen above, wave solutions for system (1.1) have been reformulated in terms of (3.9). This will now give another very useful alternative formulation.

LEMMA 3.7. *Let Assumption* 2.1 *be satisfied and assume that $R_0 > 1$. Let $c > 0$ and let u be a positive solution of* (3.9)*. Then the map $\widehat{U} \equiv \widehat{U}(x, y)$ defined by*

$$\widehat{U}(x, y) = \frac{\sigma}{c} \int_x^\infty u(l, y) dy$$

is a nonincreasing—with respect to x—solution of the equation

$$(3.10)\qquad \begin{aligned} &-(\Delta + c\partial_x - \alpha)\, \widehat{U}(x, y) = \sigma S_0(y) \int_0^\infty \beta(l) \left(1 - e^{-\widehat{U}(x+cl, y)}\right) dl,\\ &\nabla_y \widehat{U}(x, y) \cdot \nu_\Omega(y) = 0, \ \ x \in \mathbb{R}, \ y \in \partial\Omega,\\ &\lim_{x\to\infty} \widehat{U}(x, y) = 0, \ \ \lim_{x\to-\infty} \widehat{U}(x, y) = U^*(y) \ \ \forall y \in \Omega. \end{aligned}$$

On the other hand, if $\widehat{U}$ is a nonincreasing solution of (3.10) *for some $c > 0$, then $u \equiv u(x, y)$ defined by*

$$u(x, y) = -\frac{c}{\sigma} \partial_x \widehat{U}(x, y)$$

is a positive solution of (3.9) *with $c > 0$.*

The proof of this result exactly follows the same argument as that of Lemma 3.5.

3.3. Basic properties of a characteristic equation. In this section, we introduce a characteristic equation that will be used in what follows, and we study some important properties of this last equation. Let $S_0 \equiv S_0(y) \in L_+^\infty(\Omega) \setminus \{0\}$ be given. Recalling definition (2.1), we consider the function $\mathcal{L} : [0, \infty) \times [0, \infty) \to \mathbb{R}$ defined by

$$(3.11)\qquad \mathcal{L}(\lambda, c) = \lambda^2 - c\lambda - \alpha + \Lambda\left(\sigma \widehat{\beta}(c\lambda) S_0(\cdot)\right),$$

where we have set for each function $\delta \in L^1(0, \infty) \cap L^\infty(0, \infty)$, $\widehat{\delta} : [0, \infty) \to \mathbb{R}$ the Laplace transform of δ, that is,

$$\widehat{\delta}(s) = \int_0^\infty \delta(l) e^{-sl} dl \ \ \forall s \in [0, \infty).$$

Let us notice that for each $(\lambda, c) \in [0, \infty)^2$ the quantity $\mathcal{L}(\lambda, c)$ is the principal eigenvalue of the following elliptic operator acting on $W^{2,\infty}\left(\overline{\Omega}\right)$:

$$A_{\lambda,c}\varphi = \Delta_y \varphi + \left(\lambda^2 - c\lambda - \alpha + \sigma\widehat{\beta}(\lambda c)S_0(y)\right)\varphi, \tag{3.12}$$

supplemented with Neumann homogeneous boundary conditions.

Then the following useful lemma holds true.

LEMMA 3.8. *We have the following:*

(i) *For each $c \geq 0$, the map $\lambda \to \mathcal{L}(\lambda, c)$ is convex.*

(ii) *For each $\lambda > 0$, the map $c \to \mathcal{L}(\lambda, c)$ is nonincreasing.*

(iii) *Recalling definition* (2.2)*, if $R_0 > 1$, there exists a unique $c^* > 0$ such that*

$$\mathcal{L}(\lambda, c) > 0 \ \ \forall \lambda \geq 0 \text{ for any } c \in [0, c^*),$$

and for each $c > c^*$, the equation $\mathcal{L}(\lambda, c) = 0$ has two solutions, $0 < \lambda_1(c) < \lambda_2(c)$.

Proof. The proof of this result relies on the variational representation of $\mathcal{L}$. Indeed let us recall that, for each function $\gamma \in L^\infty(\Omega)$, one has

$$\Lambda(\gamma) = -\inf_{\varphi \in H^1(\Omega),\ \|\varphi\|_{L^2(\Omega)}=1} \left\{\int_\Omega |\nabla\varphi(y)|^2 - \gamma(y)\varphi(y)^2 dy\right\}.$$

We refer the reader to, for instance, Theorem 11.4 in [36] for the proof of such a variational formula. As a consequence, for each $(\lambda, c) \in [0, \infty)^2$, one has

$$-\mathcal{L}(\lambda, c) = \inf_{\substack{u \in H^1(\Omega)\\ \|u\|_{L^2(\Omega)}=1}} \left\{\int_\Omega \left(|\nabla u(y)|^2 - \left(\lambda^2 - c\lambda - \alpha + \sigma\widehat{\beta}(\lambda c)S_0(y)\right)u^2(y)\right)dy\right\}. \tag{3.13}$$

Recalling that the infimum of concave functions is also concave, (i) follows. The same argument applies for decreasing maps, so that (ii) holds true. Finally, (iii) follows from (i) and (ii) since $\mathcal{L}(0, c) \equiv \alpha\,(R_0 - 1) > 0$ and

$$\begin{cases} \lim_{c\to\infty} \mathcal{L}(\lambda, c) = -\infty \ \forall \lambda > 0 \text{ and} \\ \lim_{\lambda\to\infty} \mathcal{L}(\lambda, c) = \infty \ \forall c \geq 0. \end{cases}$$

This completes the proof of the lemma. ∎

From the above lemma, one can state the following definition.

DEFINITION 3.9 (minimal wave speed). *If $R_0 > 1$, we set*

$$c^* = \inf\left\{c > 0 : \ \exists \lambda > 0 \ \ \mathcal{L}(\lambda, c) < 0\right\}.$$

According to (iii) *in Lemma* 3.8*, we have $c^* \in (0, \infty)$. This quantity is referred to as the minimal wave speed.*

From the above definition as well as definition (3.11), it is easy to check that c^* is also defined by

$$c^* = \frac{1}{\sqrt{\Gamma}},$$

wherein Γ is defined in (2.4).

4. Spreading speed properties. The aim of this section is to prove Theorems 2.3 and 2.4.

4.1. The case $R_0 \leq 1$. The aim of this section is to prove Theorem 2.3. The dynamical properties of (1.1)–(1.3) when $R_0 \leq 1$ are rather simple, and the epizootic cannot propagate and uniformly dies out. In order to prove this result we will first prove the following lemma.

LEMMA 4.1. *Let Assumptions* 2.1 *and* 2.2 *be satisfied and assume that* $R_0 \leq 1$. *Let* $\{t_k\}_{k\geq 0}$ *be a given sequence of positive numbers tending to* ∞ *as* $k \to \infty$. *Let* $\{x_k\}_{k\geq 0}$ *be a sequence of real numbers such that* $|x_k| \to \infty$ *as* $k \to \infty$. *Then one has up to a subsequence*

$$\lim_{k\to\infty} U(t+t_k, x+x_k, y) = 0 \textit{ locally uniformly for } (t,x,y) \in \mathbb{R} \times \overline{\Sigma},$$

where U *is the solution of* (3.5).

Proof. Assume, without loss of generality, that $x_k \to \infty$ as $k \to \infty$. Then consider the sequence of map $\{U_k\}$ defined by $U_k(t,x,y) = U(t+t_k, x+x_k, y)$, which satisfies

$$\begin{aligned} &(\partial_t - \Delta_{x,y} + \alpha)\, U_k(t,x,y) = \sigma \int_0^{t+t_k} \beta(a) S_0(y) \left(1 - e^{-U_k(t-a,x,y)}\right) da \\ &\qquad\qquad\qquad\qquad\qquad + u_0(t+t_k, x+x_k, y), \\ &\nabla_y U_k(t,x,y)\cdot \nu_\Omega(y) = 0, \quad t > -t_k,\ x \in \mathbb{R},\ y \in \partial\Omega, \\ &U_k(-t_k, x, y) \equiv 0. \end{aligned} \tag{4.1}$$

Note that for each $k \geq 0$, U_k is increasing with respect to time. Due to Lemma 3.2 and parabolic regularity, one may assume that $\{U_k\}_{k\geq 0}$ converges to some function $U_\infty \equiv U_\infty(t,x,y)$ locally uniformly for $(t,x,y) \in \mathbb{R} \times \overline{\Sigma}$, which satisfies

$$\begin{aligned} &(\partial_t - \Delta_{x,y} + \alpha)\, U_\infty(t,x,y) = \sigma \int_0^{\infty} \beta(a) S_0(y) \left(1 - e^{-U_\infty(t-a,x,y)}\right) da, \\ &\nabla_y U_\infty(t,x,y)\cdot \nu_\Omega(y) = 0, \quad t \in \mathbb{R},\ x \in \mathbb{R},\ y \in \partial\Omega. \end{aligned} \tag{4.2}$$

We claim that $U_\infty \equiv 0$. To prove this, since U_∞ is increasing with respect to time, let us consider

$$\widehat{U}(x,y) := \lim_{t\to\infty} U_\infty(t,x,y).$$

Note that it satisfies

$$\begin{aligned} &(-\Delta_{x,y} + \alpha)\, \widehat{U}(x,y) = \sigma \int_0^{\infty} \beta(a) da S_0(y) \left(1 - e^{-\widehat{U}(x,y)}\right), \\ &\nabla_y \widehat{U}(x,y)\cdot \nu_\Omega(y) = 0, \quad t \in \mathbb{R},\ x \in \mathbb{R},\ y \in \partial\Omega. \end{aligned} \tag{4.3}$$

Since $R_0 \leq 1$, the only positive solution of the above equation is the zero solution $\widehat{U} \equiv 0$, and the result follows. ∎

It remains to prove Theorem 2.3.

Proof of Theorem 2.3. We will first prove that the C-component uniformly dies out. Let us first notice that since the $U(t,x,y)$ is uniformly bounded, and due to the definition of U, one obtains that

$$\lim_{t\to\infty} C(t,x,y) = 0 \text{ locally uniformly for } (x,y) \in \overline{\Sigma}.$$

Assume that there exists a sequence $(x_k, y_k) \in (0,\infty) \times \overline{\Sigma}$ with $t_k \to \infty$ and

$$\liminf_{k\to\infty} C(t_k, x_k, y_k) > 0.$$

Due to the aforementioned remark, one obtains that $|x_k| \to \infty$. Next consider $U_k(t,x,y) := U(t+t_k, x+x_k, y)$. Then, due to Lemma 3.2 and parabolic regularity, one gets that $\partial_t U_k(0,0,y_k) \to 0$ as $k \to \infty$, a contradiction. This completes the proof of the result for the C-component of the system.

To complete the proof of Theorem 2.3, it remains to prove the behavior of the S- and i-components. Let $\varepsilon : [0,\infty) \to [0,\infty)$ be a given function such that $\varepsilon(t) \to \infty$ as $t \to \infty$. Then according to Lemma 4.1 one obtains that

$$\lim_{t\to\infty} \sup_{|x|\geq\varepsilon(t),\, y\in\overline{\Omega}} U(t,x,y) = 0.$$

The result therefore follows from the expression of S given in Definition 3.2. The result for the i-component directly follows from the expression of i given in (3.3). ∎

4.2. Outer spreading speed. The following lemma holds true.

LEMMA 4.2. *Let Assumptions* 2.1 *and* 2.2 *be satisfied. Assume furthermore that* $R_0 > 1$. *Then for each* $c > c^*$ *defined in* (2.5) *one has*

$$\lim_{t\to\infty} \sup_{|x|\geq ct} \sup_{y\in\overline{\Omega}} U(t,x,y)ds = 0,$$

where U *is the solution of* (3.5).

Proof. Let $c > c^*$ be given. According to Definition 3.9, there exists $\lambda > 0$ such that

$$\mathcal{L}(\lambda, c) < 0.$$

Let $\varphi > 0$ be defined as

$$\Delta\varphi + \sigma\widehat{\beta}(c\lambda)S_0(y)\varphi = \Lambda\left(\sigma\widehat{\beta}(c\lambda)S_0(\cdot)\right)\varphi.$$

Consider the map $\overline{U}(t,x,y) = Me^{-\lambda(x-ct)}\varphi(y)$, where $M > 0$ constant that will be chosen latter on so that

$$(\partial_t - \Delta_{x,y} + \alpha)\,\overline{U}(t,x,y) - \sigma\int_0^t \beta(a)S_0(y)\overline{U}(t-a,x,y)da - u_0(t,x,y) \geq 0.$$

This leads us to

$$\begin{aligned}&\left\{c\lambda - \lambda^2 + \alpha + \sigma\widehat{\beta}(c\lambda)S_0(y) - \Lambda\left(\sigma\widehat{\beta}(c\lambda)S_0(\cdot)\right)\right\}e^{-\lambda(x-ct)}\varphi(y)\\ &- e^{-\lambda(x-ct)}\varphi(y)\sigma\int_0^t \beta(a)S_0(y)e^{-c\lambda a} - \frac{1}{M}u_0(t,x,y) \geq 0.\end{aligned}$$

This can be rewritten as

$$\begin{aligned}&- \mathcal{L}(\lambda,c)e^{-\lambda(x-ct)}\varphi(y)\\ &+ \sigma S_0(y)e^{-\lambda(x-ct)}\varphi(y)\left\{\widehat{\beta}(c\lambda) - \int_0^t \beta(a)e^{-c\lambda a}da\right\}\\ &- \frac{1}{M}u_0(t,x,y) \geq 0.\end{aligned}$$

Now according to Assumption 2.2 there exists some constant N such that

$$u_0(t,x,y) \leq Ne^{-\lambda x}\varphi(y)\ \forall (x,y) \in \overline{\Sigma},$$

so that it is sufficient to have

$$-\mathcal{L}(\lambda,c)e^{\lambda ct} + \sigma S_0(y)e^{\lambda ct}\left\{\int_t^\infty \beta(a)e^{-\lambda a}da\right\} \geq \frac{N}{M}.$$

Since $-\mathcal{L}(\lambda,c) > 0$, the result follows when $M > 0$ is large enough. ☐

Using the same supersolution argument, one can derive the following result for the C-equation.

LEMMA 4.3. *Let Assumptions* 2.1 *and* 2.2 *be satisfied. Then for each* $c > c^*$ *one has*

$$\lim_{t\to\infty} \sup_{|x|\geq ct} \sup_{y\in\overline{\Omega}} C(t,x,y)ds = 0.$$

If furthermore $i_0 \equiv 0$*, then there exists* $M > 0$ *such that*

$$C(t,x,y) \leq Me^{-\lambda^*(x-c^*t)},$$

where $\lambda^* > 0$ *satisfies*

$$\mathcal{L}(\lambda^*, c^*) = 0.$$

This lemma completes the proof of Theorem 2.4 (i) for the C-component. The proof of the outer spreading speed for the i-component comes from (3.3). Let us also notice that using such a formulation for i, one can also obtain that for each $\tau \geq 0$, $h > 0$, and $c > c^*$,

$$\lim_{t\to\infty} \sup_{|x|\geq ct;\ y\in\Omega} \int_\tau^{\tau+h} i(t,a,x,y)da = 0.$$

Note that the outer spreading speed for the S-component (namely, Theorem 2.4 (iii)) follows from the expression of S given in Definition 3.1.

4.3. Inner spreading speed and consequences. The aim of this section is to deal with the inner spreading speed and discuss some important consequences of this. Our first result relies on deriving the inner spreading speed for function U, the solution of (3.5). The result reads as follows.

THEOREM 4.4. *Let Assumptions* 2.1 *and* 2.2 *be satisfied. Assume furthermore that* $R_0 > 1$*. Then for each* $c \in (0, c^*)$ *one has*

$$\liminf_{t\to\infty} \inf_{|x|\leq ct} U(t,x,y) \geq U^*(y),$$

uniformly with respect to $y \in \overline{\Omega}$*. Here remember that* U^* *is the unique nonnegative solution provided by Lemma* 3.6*.*

The proof of this result will rely on the introduction of a suitable and well-known auxiliary reaction-diffusion equation with time delay to compare with the solution U. Do to this, for each $\tau > 0$ and $\delta \in [0,1)$, let us consider

$$R(\tau,\delta) = \frac{1}{\alpha}\Lambda\left(\sigma(1-\delta)\int_0^\tau \beta(a)daS_0(\cdot)\right).$$

Since $R_0 > 1$, there exists $\tau_0 > 0$ and $\delta_0 > 0$ such that

$$R(\tau,\delta) > 1 \ \ \forall \tau > \tau_0,\ \delta \in (0,\delta_0).$$

Next, for each $\tau > \tau_0$ and $\delta \in (0,\delta_0)$, consider the map

$$\mathcal{L}_{\tau,\delta}(\lambda,c) = \lambda^2 - c\lambda - \alpha + \Lambda\left((1-\delta)\sigma\widehat{\beta 1_{(0,\tau)}}(c\lambda)S_0(\cdot)\right),$$

and let us define $c^*_{\tau,\delta}$ similarly to c^* (see Definition 3.9).

LEMMA 4.5. *One has for each* $\tau > \tau_0$

$$c^*_{\tau,\delta} \nearrow c^*_{\tau,0} \text{ as } \delta \searrow 0$$

and

$$c^*_{\tau,0} \nearrow c^* \text{ as } \tau \nearrow \infty.$$

Proof. Let $\tau > \tau_0$ be given. Then since $\mathcal{L}_{\tau,\delta} \le \mathcal{L}_{\tau,0} \le \mathcal{L}$, one obtains from the definition of c^* that

$$c^*_{\tau,\delta} \le c^*_{\tau,0} \ \ \forall \delta \in [0,\delta_0).$$

Consider a sequence $\{\delta_n\}_{n\ge 0} \subset [0,\delta_0)$ that is decreasing and tends to zero. Next consider the following for each $n \ge 0$: $c^*_n := c^*_{\tau,\delta_n}$. Since $\mathcal{L}_{\tau,\delta}$ is decreasing with respect to δ, it is easy to see that the sequence $\{c^*_n\}_{n\ge 0}$ is increasing. Furthermore, from the definition of c^*_n, for each $n \ge 0$ there exists $\lambda_n > 0$ such that

$$\mathcal{L}_{\tau,\delta_n}(\lambda_n, c_n) = 0.$$

Therefore $\lambda_n^2 - c^*_n\lambda_n - \alpha \le 0$ so that $\{\lambda_n\}_{n\ge 0}$ is bounded. Up to a subsequence, one may assume that $\lambda_n \to \lambda_\infty \ge 0$, so that if we denote by $\widehat{c} := \lim_{n\to\infty} c^*_n$, one has

$$\mathcal{L}_{\tau,0}\left(\lambda_\infty, \widehat{c}\right) = 0.$$

As a consequence, one obtains that $c^*_\tau \ge \widehat{c}$ and the result follows. ∎

Next let us consider the following auxiliary reaction-diffusion equation with time delay:

$$\begin{aligned} &(\partial_t - \Delta + \alpha)\, V(t,x,y) = \sigma S_0(y)\int_{-\tau}^{0} \beta(-\theta) f\left(V_t(\theta,x,y)\right) d\theta,\ t>0,\ (x,y)\in\Sigma, \\ &\nabla_y V(t,x,y)\cdot \nu_\Omega(y) = 0,\ \ t>0,\ (x,y)\in \mathbb{R}\times\partial\Omega, \end{aligned} \tag{4.4}$$

supplemented with some initial datum

$$V_0(\theta,x,y) = v_0(\theta,x,y),\ \ (\theta,(x,y)) \in [-\tau,0]\times\overline{\Sigma}.$$

Here we have set $V_t(\theta,x,y) = V(t+\theta,x,y)$.

From the theory developed by Liang and Zhao in [21] and the first property in Lemma 4.5, the following result holds true.

LEMMA 4.6. *Let Assumption* 2.1 *be satisfied. Let* $\tau > \tau_0$ *be given. Then for each* $c \in \left(0, c^*_{\tau,0}\right)$ *and each* $v_0 \equiv v_0(\theta,x,y)$ *belonging in* $C_+\left([-\tau,0]; C\left(\overline{\Sigma}\right)\right) \setminus \{0\}$, *there exists* $\delta > 0$ *such that*

$$\liminf_{t\to\infty}\ \inf_{|x|\le ct,\ y\in\Omega} V(t,x,y) \ge \delta.$$

We are now able to use (4.4) as well as Lemma 4.6 to prove the following first result.

LEMMA 4.7. *Let Assumptions* 2.1 *and* 2.2 *be satisfied. Assume furthermore that* $R_0 > 1$. *Then for each* $c \in (0, c^*)$ *there exists* $\delta > 0$ *such that*

$$\liminf_{t\to\infty} \inf_{|x|\le ct,\ y\in\Omega} U(t,x,y) \ge \delta.$$

Proof. Let $c \in (0, c^*)$ be given. Then according to Lemma 4.5, there exists $\tau > 0$ large enough such that

$$c < c^*_{\tau,0}.$$

Consider U as a solution of (3.5). Then for each $t > \tau$ one has

$$(\partial_t - \Delta + \alpha)\, U(t,x) - \sigma S_0(y) \int_0^\tau \beta(a) f\left(U(t-a,x,y)\right) \ge 0.$$

As a consequence, if we choose $v_0 \equiv v_0(\theta,x,y)$ such that

$$v_0 \in C_+\left([-\tau,0]; C\left(\overline{\Sigma}\right)\right) \setminus \{0\},$$
$$v_0(\theta,x,y) \le U(\tau+\theta,x,y) \ \ \forall (\theta,x,y) \in [-\tau,0] \times \overline{\Sigma},$$

one obtains from the comparison principle that

$$V_t(\theta,x,y) \le U(t+\tau+\theta,x,y) \ \ \forall t \ge 0,\ \forall (\theta,x,y) \in [-\tau,0] \times \overline{\Sigma},$$

wherein V_t denotes the solution of (4.4) with initial datum v_0. Since $c \in \left(0, c^*_{\tau,0}\right)$, the result follows by applying Lemma 4.6. $\square$

Next let us prove the following lemma.

LEMMA 4.8. *Let Assumption* 2.1 *be satisfied. Assume that there exists* $c_0 > 0$ *and* $\delta > 0$ *such that*

$$\liminf_{t\to\infty} \inf_{|x|\le c_0 t,\ y\in\Omega} U(t,x,y) \ge \delta.$$

Then for each sequence $\{t_k\}$ *tending to* ∞ *and* $\{x_k\} \subset \mathbb{R}$ *such that*

$$\lim_{k\to\infty} |x_k| = \infty \quad \textit{and} \quad \limsup_{k\to\infty} \frac{|x_k|}{t_k} < c_0,$$

up to a subsequence one has

$$\lim_{k\to\infty} U(t+t_k, x+x_k, y) = U^*(y)$$

locally uniformly for $(t,x,y) \in \mathbb{R} \times \overline{\Sigma}$.

Proof. Let us notice that for each $(t,x,y) \in \mathbb{R} \times \overline{\Sigma}$ there exists $k_0 > 0$ large enough such that

$$|x + x_k| < c_0(t+t_k) \ \ \forall k \ge k_0.$$

As a consequence, if we set $U_k(t,x,y) := U(t+t_k, x+x_k, y)$, one obtains that for each $(t,x,y) \in \mathbb{R} \times \overline{\Sigma}$, there exists $k_1 > 0$ large enough such that

$$U_k(t,x,y) \ge \frac{\delta}{2}.$$

Due to this property as well as parabolic estimates, one may assume (possibly up to a subsequence) that $U_k(t,x,y)$ converges locally uniformly to some function $U_\infty(t,x,y)$ satisfying

$$U_\infty(t,x,y) \geq \frac{\delta}{2} \ \ \forall (t,x,y) \in \mathbb{R}\times\overline{\Sigma},$$

and since $|x_k| \to \infty$, U_∞ satisfies, for all $(t,x,y)\in\mathbb{R}\times\overline{\Sigma}$,

$$\begin{aligned}&(\partial_t - \Delta_{x,y} + \alpha)\, U_\infty(t,x,y) = \sigma S_0(y)\int_0^\infty \beta(a)\left(1-e^{-U_\infty(t-a,x,y)}\right)da,\\ &\nabla_y U_\infty(t,x,y)\cdot \nu_\Omega(y) = 0, \ \ (t,x,y)\in\mathbb{R}\times\mathbb{R}\times\partial\Omega.\end{aligned}$$

Then one obtains that $U_\infty(t,x,y)\equiv U^*(y)$ and the result follows. ◻

As a consequence, one obtains the following result that completes the proof of Theorem 4.4.

LEMMA 4.9. *Let Assumption* 2.1 *be satisfied. Assume that there exist* $c_0>0$ *and* $\delta>0$ *such that*

$$\liminf_{t\to\infty}\inf_{|x|\leq c_0 t,\ y\in\Omega} U(t,x,y)\geq\delta.$$

Then one has for each $c\in(0,c_0)$

$$\liminf_{t\to\infty}\inf_{|x|\leq ct} U(t,x,y)\geq U^*(y)$$

uniformly with respect to $y\in\overline{\Omega}$.

Proof. Let us argue by contradiction by assuming that there exist $c\in(0,c_0)$, a sequence $\{t_k\}_{k\geq 0}$ tending to infinity as $k\to\infty$, a sequence $\{x_k\}_{k\geq0}$ with $|x_k|\leq ct_k$, $\{y_k\}\subset\overline{\Omega}$, and $\varepsilon>0$ such that

$$U(t_k,x_k,y_k) < U^*(y_k)-\varepsilon \ \ \forall k\geq 0. \tag{4.5}$$

Let us first assume that up to a subsequence, $|x_k|\to\infty$ as $k\to\infty$ while $y_k\to y_\infty\in\overline{\Omega}$ as $k\to\infty$. Then due to Lemma 4.8 one gets

$$\lim_{k\to\infty} U(t_k,x_k,y_k) = U^*(y_\infty),$$

a contradiction. As a consequence, the sequence $\{x_k\}$ is bounded, and up to a subsequence, it converges to x_∞ while $y_k\to y_\infty$. Next recall that U is increasing with respect to time and uniformly bounded due to Lemma 3.2 so that there exists a map $\overline{U}\equiv\overline{U}(x,y)$ such that

$$\lim_{t\to\infty} U(t,x,y) = \overline{U}(x,y)$$

locally uniformly for $(x,y)\in\overline{\Sigma}$ and where $\overline{U}$ satisfies

$$\begin{aligned}&(-\Delta_{x,y}+\alpha)\,\overline{U}(x,y) = \sigma\int_0^\infty \beta(a)daS_0(x,y)\left(1-e^{-\overline{U}(x,y)}\right)da + \widehat{u}_0(x,y),\\ &\nabla_y\overline{U}(x,y)\cdot\nu_\Omega(y)=0, \ \ x\in\mathbb{R},\ y\in\partial\Omega,\end{aligned}$$

and wherein we have set

$$\widehat{u}_0(x,y) = \sigma\left(C_0(x,y)+\int_0^\infty\int_s^\infty \beta(a) i_0(a-s,x,y)dads\right).$$

Since $\widehat{u}_0 \geq 0$, one obtains that $\overline{U}(x,y) \geq U^*(y)$ and therefore

$$\lim_{k\to\infty} U(t_k, x_k, y_k) = \overline{U}\left(x_\infty, y_\infty\right) \geq U^*\left(y_\infty\right),$$

a contradiction with (4.5). The result follows. □

In order to prove that the C-component has an asymptotic pulse shape, let us prove the following result.

LEMMA 4.10. *Let Assumption* 2.1 *be satisfied. Assume that there exist* $c_0 > 0$ *and* $\delta > 0$ *such that*

$$\liminf_{t\to\infty} \inf_{|x|\leq c_0 t,\ y\in\Omega} U(t,x,y) \geq \delta.$$

Then one has for each $c \in (0, c_0)$

$$\lim_{t\to\infty} \sup_{|x|\leq ct,\ y\in\Omega} C(t,x,y) = 0.$$

This result follows from Lemma 4.8 together with the same arguments as that of Lemma 4.9. The details are left to the reader. Note that this lemma completes the proof of Theorem 2.4 (ii) for the C-component. Once again, the proof of the behavior for i-component comes from (3.3), while the inner spreading speed for the S-component (namely, Theorem 2.4 (iv)) follows from the expression of S given in Definition 3.2. Here again, using such a formulation for i, one can also obtain that for each $\tau \geq 0$, $h > 0$, and $c \in (0, c^*)$,

$$\lim_{t\to\infty} \sup_{|x|\leq ct;\ y\in\Omega} \int_\tau^{\tau+h} i(t,a,x,y)da = 0.$$

We are now able to prove the first part of Theorem 2.4, which is the persistence of the disease.

Proof of the first part of Theorem 2.4*:* (2.6) *and* (2.7). Let us first derive a stronger result than the one stated in (2.6). To be more precise, let us prove that the following lemma holds true.

LEMMA 4.11 (stronger form of (2.6)). *Let Assumptions* 2.2 *and* 2.1 *be satisfied. If* $R_0 > 1$*, then the epizootic persists, in the sense that*

$$\liminf_{t\to\infty} \sup_{x\in\mathbb{R}} \min_{y\in\overline{\Omega}} C(t,x,y) > 0.$$

Proof. We will argue by contradiction by assuming that there exists a sequence $\{t_k\}_{k\geq 0}$ tending to infinity as $k \to \infty$ and such that

$$\liminf_{k\to\infty} \sup_{x\in\mathbb{R}} \min_{y\in\overline{\Omega}} C\left(t_k, x, y\right) = 0.$$

Note that due to the spreading speed property for U provided by Theorem 4.4 and Lemma 4.2, for each $\varepsilon > 0$, there exists a sequence $\{x_k\}_{k\geq 0} \subset \mathbb{R}$ such that for all $y \in \overline{\Omega}$

$$\varepsilon \leq U(t_k, x_k, y) \leq \inf_{y\in\overline{\Omega}} U^*(y) - \varepsilon, \tag{4.6}$$

where U^* is provided by Lemma 3.6. For each $k \geq 0$, consider $\{y_k\} \subset \overline{\Omega}$ such that

$$\min_{y\in\overline{\Omega}} C\left(t_k, x_k, y\right) = C\left(t_k, x_k, y_k\right).$$

Without loss of generality, one may assume

$$\lim_{k\to\infty} y_k = y_\infty \in \overline{\Omega}.$$

Consider now the sequence of map $U_k(t,x,y) = U(t+t_k, x+x_k, y)$. Then it satisfies

$$\begin{aligned}
&(\partial_t - \Delta + \alpha)\, U_k(t,x,y) = \sigma S_0(y) \int_0^\infty \beta(a) \left(1 - e^{-U_k(t-a,x,y)}\right) da,\\
&\nabla_y U_k(t,x,y)\cdot \nu_\Omega(y) = 0,\ \ (t,x,y) \in (-t_k,\infty)\times\mathbb{R}\times\partial\Omega.
\end{aligned}$$

Due to parabolic estimates, one may assume that $U_k \to U_\infty$, for some function U_∞, locally uniformly. Furthermore, if we remember that

$$U_k(t,x,y) = \int_0^{t+t_k} C(s, x+x_k, y) ds,$$

one concludes that

$$\partial_t U_k(t,x,y) = C(t+t_k, x+x_k, y),$$

so that, due to the definition of $\{y_k\}$,

$$\partial_t U_\infty(0,x,y_\infty) \equiv 0,$$

and due to (4.6), U_∞ satisfies for each $y \in \overline{\Omega}$

$$\varepsilon \le U_\infty(0,0,y) \le \inf_{y\in\overline{\Omega}} U^*(y) - \varepsilon,$$

while U_∞ satisfies

$$\begin{aligned}
&(\partial_t - \Delta_{x,y} + \alpha)\, U_\infty(t,x,y) = \sigma S_0(y) \int_0^\infty \beta(a) \left(1 - e^{-U_\infty(t-a,x,y)}\right) da,\\
&\nabla_y U_\infty(t,x,y)\cdot \nu_\Omega(y) = 0,\ \ (t,x,y) \in \mathbb{R}\times\mathbb{R}\times\partial\Omega.
\end{aligned}$$

Let us notice that the condition $\partial_t U_\infty(0,x,y_\infty) \equiv 0$ together with the strong comparison principle implies that

$$\partial_t U_\infty(t,x,y) \equiv 0\ \ \forall (t,x,y) \in \mathbb{R}\times\mathbb{R}\times\overline{\Omega},$$

so that $U_\infty(t,x,y) \equiv U_\infty(x,y)$, which satisfies

$$\varepsilon \le U_\infty(0,y) \le \inf_{y\in\overline{\Omega}} U^*(y) - \varepsilon, \tag{4.7}$$

while U_∞ satisfies

$$\begin{aligned}
&(\alpha - \Delta_{x,y})\, U_\infty(x,y) = \sigma S_0(y) \int_0^\infty \beta(a) da \left(1 - e^{-U_\infty(x,y)}\right),\\
&\nabla_y U_\infty(x,y)\cdot \nu_\Omega(y) = 0,\ \ (x,y) \in \mathbb{R}\times\mathbb{R}\times\partial\Omega.
\end{aligned}$$

If one finally considers a smooth positive function $w_0 \equiv w_0(x,y)$ such that

$$w_0(x,y) \le U_\infty(x,y),\ \ \forall (x,y) \in \overline{\Sigma},$$

(note that the latter is possible since $U_\infty \not\equiv 0$ (see (4.7))), due to the comparison principle, one obtains that

$$w(t,x,y) \leq U_\infty(x,y) \ \ \forall (t,x,y) \in [0,\infty) \times \overline{\Sigma},$$

wherein we have set w as the solution of the Fisher-KPP equation:

$$\begin{aligned}
&(\partial_t - \Delta_{x,y} + \alpha)\, w(t,x,y) = \sigma S_0(y) \int_0^\infty \beta(a)da \left(1 - e^{-w(t,x,y)}\right),\\
&\nabla_y w(t,x,y) \cdot \nu_\Omega(y) = 0, \ \ (t,x,y) \in (0,\infty) \times \mathbb{R} \times \partial\Omega,\\
&w(0,x,y) = w_0(x,y).
\end{aligned}$$

Recall that $R_0 > 1$ and $w_0 \not\equiv 0$, so that

$$\lim_{t\to\infty} w(t,x,y) = U^*(y) \text{ locally uniformly},$$

and therefore $U^*(y) \leq U_\infty(x,y)$ for all $(x,y) \in \overline{\Sigma}$, a contradiction with (4.7). This completes the proof of the lemma and therefore (2.6). □

In order to consider the proof of (2.7), recall that relation (ii) of Definition 3.1 holds true. Then according to Lemma 3.2 there exists some constant $K > 0$ such that for all $t > 0$, $(x,y) \in \Sigma$,

$$i(t,0,x,y) \geq K S_0(y) C(t,x,y) \geq K S_0(y) \min_{y\in\overline{\Omega}} C(t,x,y).$$

Then for each $\varphi \in L^1_+(\Omega)$ one has

$$\int_\Omega \varphi(y) i(t,0,x,y)dy \geq K \left(\int_\Omega \varphi(y) S_0(y)dy\right) \min_{y\in\overline{\Omega}} C(t,x,y).$$

If we set $\delta > 0$ defined by

$$\delta := \liminf_{t\to\infty} \sup_{x\in\mathbb{R}} \min_{y\in\overline{\Omega}} C(t,x,y),$$

then (2.7) follows. □

Remark 4.12. Using once again the formula (ii) in Definition 3.1, one can prove that there exists $\delta > 0$ such that for each $\tau \geq 0$ and $h > 0$ one has for each $\varphi \in L^1_+(\Omega)$

$$\liminf_{t\to\infty} \sup_{x\in\mathbb{R}} \int_\Omega \int_\tau^{\tau+h} \varphi(y) i(t,a,x,y)dady \geq h\delta \int_\Omega \varphi(y) S_0(y)dy.$$

5. Proofs of Theorems 2.6 and 2.7.

5.1. Proof of Theorem 2.6. The proof of the existence of traveling wave solutions for system (1.1) is strongly related to Lemma 3.7. According to this reformulation, to prove Theorem 2.6, it is sufficient to prove the following lemma.

LEMMA 5.1. *Let Assumption* 2.1 *be satisfied. Let* $S_0 \in L^\infty_+(\Omega)$ *be given and assume that* $R_0 > 1$. *Then for each* $c \geq c^*$, *system* (3.10) *has a nonincreasing solution* $\widehat{U}$.

Due to the applicability of the comparison principle for this nonlocal elliptic problem, the proof of this result is standard. The case $c > c^*$ can be handled by the construction of suitable sub- and supersolutions. The problem is then solved by using a monotone iterative scheme. The case $c = c^*$ is obtained by passing to the limit $c \searrow c^*$ and using an arbitrary normalization of the solution to take care of the translation invariance. We refer the reader to, for instance, the works of Diekmann [9, 10], Liang and Zhao [21], Thieme and Zhao [41], the monograph of Rass and Radcliffe [34] (and the references cited therein), and Zou and Wu [52] (we also refer the reader to [11, 12, 23, 47] and the references cited therein for examples of fixed point arguments).

Here we will only give a sketch of the proof in the case $c > c^*$ and, more precisely, we only focus on the construction of suitable sub- and supersolutions for system (3.10).

Let $c > c^*$ be given and fixed. Since $c > c^*$, according to Definition 3.9 and Lemma 3.8 (iii), the equation $\mathcal{L}(\lambda, c) = 0$ has two solutions denoted by $0 < \lambda < \lambda^*$. Consider now an associated eigenvector $\varphi \in W^{2,\infty}(\Omega)$ corresponding to the following eigenvalue problem:

$$\begin{aligned}&\Delta\varphi + \left(\lambda^2 - c\lambda - \alpha + \sigma S_0(y)\widehat{\beta}(\lambda c)\right)\varphi = 0 \text{ in } \Omega,\\ &\nabla\varphi(y)\cdot\nu_\Omega(y) = 0, \quad y \in \partial\Omega \text{ and } \varphi > 0.\end{aligned}$$

Next consider the maps defined by

$$\overline{u}(x, y) = e^{-\lambda x}\varphi(y).$$

Then the following lemma holds true.

Lemma 5.2. *Functions* $\overline{u}$ *satisfy*

$$\begin{aligned}&-(\Delta + c\partial_x - \alpha)\,\overline{u}(x, y) = \sigma S_0(y)\int_0^\infty \beta(a)\overline{u}(x + ca, y)da,\\ &\nabla\overline{u}(x, y)\cdot\nu_\Sigma(x, y) = 0, \quad (x, y) \in \mathbb{R}\times\partial\Omega.\end{aligned}$$

According to Lemma 3.8 (iii) and due to the definition of λ, there exists $\eta \in (0, \lambda)$ such that

$$\mathcal{L}(\lambda + \eta, c) < 0.$$

Consider $\varphi_\eta \in W^{2,\infty}(\Omega)$ a nonnegative eigenvector of operator $A_{\lambda+\eta,c}$ (defined in (3.12)) associated to its principal eigenvalue $\mathcal{L}(\lambda + \eta, c)$. Then the following lemma holds true.

Lemma 5.3. *Let* $\kappa > 0$ *be given. There exists* $k = k_\kappa > 0$ *large enough such that the map*

$$w(x, y) = e^{-\lambda x}\varphi(y) - ke^{-(\lambda+\eta)x}\varphi_\eta(y)$$

satisfies

$$-(\Delta + c\partial_x + \alpha)\,w(x, y) \le \sigma S_0(y)\int_0^\infty \beta(a)w(x + ca, y)\left(1 - \kappa e^{-\lambda(x+ca)}\varphi(y)\right)^+ da \tag{5.1}$$

on the set $\{(x, y) \in \mathbb{R}\times\Omega : \; w(x, y) \ge 0\}$.

Proof. Let us set

$$x_k = \frac{1}{\eta}\ln\frac{k\inf_{\overline{\Omega}}\varphi_\eta}{\sup_{\overline{\Omega}}\varphi}. \tag{5.2}$$

Then we have

$$\Sigma_k := [x_k, \infty) \times \Omega \subset \{(x,y) \in \mathbb{R} \times \Omega : \ w(x,y) \geq 0\}.$$

We shall show that (5.1) holds true in Σ_k when k is large enough. Let us first choose $k > 0$ so that

$$1 \geq \kappa e^{-\lambda x} \varphi(y) \ \ \forall (x,y) \in \Sigma_k. \tag{5.3}$$

Next, inequality (5.1) can be rewritten for all $(x,y) \in \Sigma_k$ as

$$\begin{aligned}
&e^{-\lambda x} \left(\sigma S_0(y) \widehat{\beta}(c\lambda) \right) \varphi + k e^{-(\lambda+\eta)x} \left(\mathcal{L}(\lambda+\eta, c)\varphi_\eta - \sigma S_0(y) \widehat{\beta}\left(c(\lambda+\eta)\right) \varphi_\eta \right) \\
&\leq \sigma S_0(y) \int_0^\infty \beta(a) e^{-\lambda(x+ca)} \varphi(y) \left(1 - \kappa e^{-\lambda(x+ca)} \varphi(y) \right) da \\
&- k\sigma S_0(y) \int_0^\infty \beta(a) \sigma e^{-(\lambda+\eta)(x+ca)} \varphi_\eta(y) \left(1 - \kappa e^{-\lambda(x+ca)} \varphi(y) \right) da.
\end{aligned}$$

This in turn can be rewritten as

$$\begin{aligned}
k\mathcal{L}(\lambda+\eta, c)\varphi_\eta &\leq -\kappa\sigma S_0(y) \varphi(y)^2 e^{(\eta-\lambda)x} \int_0^\infty \beta(l) e^{-2\lambda c l} dl \\
&+ k\kappa\sigma S_0(y) \varphi_\eta(y) \varphi(y) e^{-\lambda x} \int_0^\infty \beta(l) e^{-(2\lambda+\eta)cl} dl.
\end{aligned}$$

Recalling that $\mathcal{L}(\lambda+\eta, c) < 0$, one obtains that

$$\begin{aligned}
&\kappa\sigma S_0(y)\varphi(y)^2 e^{(\eta-\lambda)x} \widehat{\beta}(2\lambda c) \\
&\leq k\varphi_\eta(y) \left\{ -\mathcal{L}(\lambda+\eta, c) + \kappa\sigma S_0(y) \varphi_\eta(y) \varphi(y) e^{-\lambda x} \widehat{\beta}\left((2\lambda+\eta)\, c\right) \right\}.
\end{aligned}$$

Therefore since $\eta - \lambda < 0$, for (5.1) to be satisfied, it is sufficient to have

$$\kappa\sigma \sup_{y\in\Omega} \{S_0(y)\varphi(y)^2\} e^{(\eta-\lambda)x_k} \widehat{\beta}(2\lambda c) \leq k \inf_\Omega \varphi_\eta \left\{ -\mathcal{L}(\lambda+\eta, c) \right\}.$$

Recalling definition (5.2), this can be rewritten as

$$\kappa\sigma \sup_{y\in\Omega} \{S_0(y)\varphi(y)^2\} \left\{ \frac{\inf_{\overline{\Omega}} \varphi_\eta}{\sup_{\overline{\Omega}} \varphi} \right\}^{1-\frac{\lambda}{\eta}} \widehat{\beta}(2\lambda c) \leq k^{\frac{\lambda}{\eta}} \inf_\Omega \varphi_\eta \left\{ -\mathcal{L}(\lambda+\eta, c) \right\}.$$

The latter inequality holds true when k is large enough. This completes the proof of the lemma. $\square$

To complete the sketch of the proof of existence of traveling waves for (3.10), let us notice that there exists $\kappa > 0$ large enough such that

$$1 - e^{-U} \geq U\left(1 - \kappa U\right) \ \ \forall U \geq 0. \tag{5.4}$$

Next we set

$$\overline{U}(x,y) = \min\left(U^*(y), \overline{u}(x,y)\right),$$

where U^* is defined by Lemma 3.6, while $\overline{u}$ is defined in Lemma 5.2. For $\kappa > 0$ defined in (5.4), we consider

$$\underline{U}(x,y) = \max\left(w(x,y), 0\right),$$

wherein w is defined in Lemma 5.3. Using these functions as sub- and supersolutions, one checks by using a monotone iterative scheme, for instance, that Lemma 5.1 holds true for any $c > c^*$. The details are left to the reader, as is the limit argument $c \searrow c^*$ used to obtain the existence of solution for this critical speed (we refer the reader to, for instance, [11] for such an argument).

5.2. Proof of Theorem 2.7. The aim of this section is to prove Theorem 2.7. The proof of this result is related to Lemma 3.7 and Theorem 4.4. Let us assume that $R_0 > 1$, and let us argue by contradiction by assuming that there exists a traveling solution of system (1.1) for some wave speed $c \in (0, c^*)$. Then according to Lemma 3.7, this implies that there exists $\widehat{U}$, a nonincreasing solution of the following equation:

$$\begin{aligned}
&-(\Delta + c\partial_x - \alpha)\,\widehat{U}(x,y) = \sigma S_0(y)\int_0^\infty \beta\,(l)\left(1 - e^{-\widehat{U}(x+cl,y)}\right)dl,\\
&\nabla_y \widehat{U}(x,y)\cdot \nu_\Omega(y) = 0, \quad x \in \mathbb{R},\ y \in \partial\Omega, \qquad (5.5)\\
&\lim_{x\to\infty} \widehat{U}(x,y) = 0, \quad \lim_{x\to-\infty} \widehat{U}(x,y) = U^*(y) \ \ \forall y \in \Omega.
\end{aligned}$$

Let us notice that the function $U(t,x,y) = \widehat{U}(x - ct, y)$ satisfies

$$\begin{aligned}
&(\partial_t - \Delta - \alpha)\,U(t,x,y) = \sigma S_0(y)\int_0^\infty \beta\,(l)\left(1 - e^{-U(t-l,x,y)}\right)dl,\\
&\nabla_y U(t,x,y)\cdot \nu_\Omega(y) = 0, \quad (t,x,y) \in \mathbb{R}\times\overline{\Sigma}.
\end{aligned}$$

This can be rewritten as

$$\begin{aligned}
&(\partial_t - \Delta - \alpha)\,U(t,x,y) = \sigma S_0(y)\int_0^t \beta\,(l)\left(1 - e^{-U(t-l,x,y)}\right)dl + U_0(t,x,y),\\
&\nabla_y U(t,x,y)\cdot \nu_\Omega(y) = 0, \quad (t,x,y) \in \mathbb{R}\times\overline{\Sigma},
\end{aligned}$$

with

$$U_0(t,x,y) = \sigma S_0(y)\int_t^\infty \beta\,(l)\left(1 - e^{-U(t-l,x,y)}\right)dl.$$

According to the spreading speed property provided by Theorem 4.4, if we choose $c_0 \in (c, c^*)$, one obtains that

$$\liminf_{t\to\infty} U(t, c_0 t, y) \geq U^*(y)$$

uniformly with respect to $y \in \overline{\Omega}$. If we come back to the definition of U in terms of function $\widehat{U}$, this can be rewritten as

$$\liminf_{t\to\infty} \widehat{U}\left((c_0 - c)\,t, y\right) \geq U^*(y).$$

However, since $c_0 - c > 0$, (5.5) provides that

$$\lim_{x\to\infty} \widehat{U}\,(x,y) = 0,$$

which leads us to a contradiction and completes the proof of Theorem 2.7.

6. Minimization of the parameter R_0 and of the propagation speed.

6.1. Proof of Theorem 2.8. The proof of Theorem 2.8 is a direct consequence of the following lemma.

Lemma 6.1. *Let* $m > 0$ *be given. Then one has*

$$\inf_{\gamma \in \mathcal{A}_{ad}(m)} \Lambda(\gamma) = \Lambda(m),$$

where

$$\mathcal{A}_{ad}(m) = \left\{ \gamma \in L^\infty_+(\Omega) : \ \frac{1}{|\Omega|} \int_\Omega \gamma(y) dy = m \right\}.$$

Proof. Let us recall that for each $\gamma \in \mathcal{A}_{ad}(m)$ one has

$$\Lambda(\gamma) = - \inf_{\varphi \in H^1(\Omega),\ \|\varphi\|_{L^2(\Omega)}=1} \left\{ \int_\Omega |\nabla \varphi(y)|^2 - \gamma(y)\varphi(y)^2 dy \right\}.$$

This implies (by taking $\varphi(y) \equiv |\Omega|^{-1/2}$) that for each $\gamma \in \mathcal{A}_{ad}(m)$

$$\Lambda(\gamma) \geq \frac{1}{|\Omega|} \int_\Omega \gamma(y) dy \geq m.$$

Thus we get that

$$m \leq \inf_{\gamma \in \mathcal{A}_{ad}(m)} \Lambda(\gamma).$$

On the other hand, one has $m \in \mathcal{A}_{ad}(m)$ and $\Lambda(m) = m$. This completes the proof of the lemma. ∎

6.2. Proof of Theorem 2.10. The aim of this section is to prove Theorem 2.10. Recalling Assumption 2.9, let us first notice that for each $L > 0$ one has

$$\Lambda(S_L) = - \inf_{\varphi \in H^1(0,1),\ \|\varphi\|_{L^2(0,1)}=1} \left\{ \frac{1}{L^2} \int_\Omega |\nabla \varphi(y)|^2 - S_0(y)\varphi(y)^2 dy \right\}.$$

Thus, the above variational formulation shows that the map $L \mapsto \Lambda(S_L)$ is increasing. Thus, due to the definition of $R_0(L)$ given in (2.2), one concludes that the map $L \mapsto R_0(L)$ is increasing. Moreover, since we have

$$\lim_{L \nearrow \infty} \Lambda(S_L) = \|S_0\|_\infty,$$

we get that

$$\lim_{L \to \infty} R_0(L) = R_0^\infty := \frac{\sigma \|S_0\|_\infty}{\alpha} \int_0^\infty \beta(l) dl.$$

The monotonic property as well as the converge of the minimal wave speed $c^*(L)$ when $L \to \infty$ follow the same arguments.

Table 7.1
Baseline values of the model parameters.

	Description	Dimension	Values	Sources
α	Mortality rate of the bacteria	Day^{-1}	0.1	[32, 33, 51]
D	Diffusion coeff. of bacterial dispersion	$\text{m}^2 \cdot \text{Day}^{-1}$	0.01	[32, 51]
θ	Normalization param. for excretion rate	$\text{cfu} \cdot \text{Day}^{-2}$	413.22	[51]
τ_1	Length of the latency period	Day	1	[42, 51]
τ_2	Length of the infectious period	Day	23	[32, 33, 51]
L_x	Length of the hen house	m	30	from [51]
L_y	Width of the hen house	m	15	from [51]
σ	Transmission rate	Day^{-1}	10^{-5}	estimated from [51]

7. Numerical experiments. In this section, we present some numerical simulations to illustrate our theoretical results. We used a finite difference method (see, e.g., [30]). The numerical scheme is detailed in the appendix and was implemented using MATLAB (www.matlab.org).

For the computation, the ideal case of an infinite domain in the x-direction will be approximated by setting $\Sigma = (0, L_x) \times \Omega$ with $\Omega = (0, L_y)$, where L_x and L_y are the length and width of the hen house, respectively. Then we supplement model equations (1.1)–(1.2) with no flux boundary conditions at $x = 0$ and $x = L_x$ by setting

$$\nabla C(t, x, y) \cdot \nu_\Sigma(x, y) = 0, \quad (t, y) \in (0, \infty) \times \mathbb{R} \times \Omega, \; x = 0, L_x. \tag{7.1}$$

We start this section by retrieving relevant values for the parameters of model (1.1)–(1.2)–(7.1) from previous works [31, 32, 33, 51].

7.1. Model calibration. The list of the parameters of our model as well as their values are summarized in Table 7.1.

The values of the the mortality rate of the bacteria, α, for the diffusion coefficient of bacteria in the environment, D, are explicitly given in [32, 33, 51] and equal 0.1 Day^{-1} and 0.01 $\text{m}^2 \cdot \text{Day}^{-1}$, respectively.

We choose the excretion rate of hens with respect to age a to be a function of the form

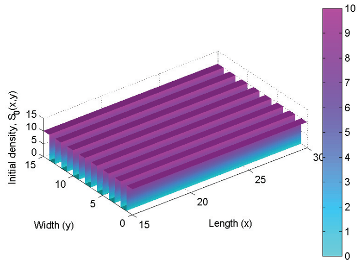
$$\beta(a) = \begin{cases} \theta \cdot (\tau_1 - a)(a - (\tau_1 + \tau_2)) & \text{if } a \in [\tau_1; \tau_1 + \tau_2], \\ 0 \quad \text{otherwise}, \end{cases} \tag{7.2}$$

where τ_1 (resp., τ_2) is the mean duration of the latency (resp., infectious) period, and θ is set to 413.22 $\text{cfu} \cdot \text{Day}^{-2}$ so that the maximal value of β equals 5.10^4 cfu (colony forming unit) as in [51]. As in [42, 51], animals begin to excrete bacteria one day post-inoculation, hence $\tau_1 = 1$ Day. Since hens excrete bacteria in the environment at digestive and systemic states, then the length of the infectious period τ_2 is the sum of the average durations of the digestive period and of the systemic period, i.e., $\tau_2 = 2 + 21 = 23$ Days from [32, 33].

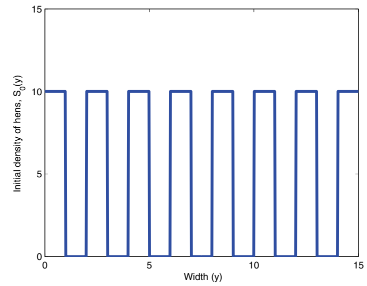
In what follows, we will focus on the density of infectious hens at time t and position (x, y) defined as

$$I(t, x, y) = \int_{\tau_1}^{\tau_1 + \tau_2} i(t, s, x, y) ds. \tag{7.3}$$

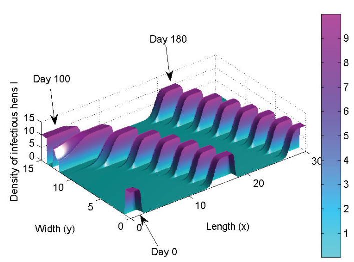
To estimate a realistic value of the disease transmission σ, we numerically reproduce the results of one of the simulation scenarios described on Figure 8(a) in [51].



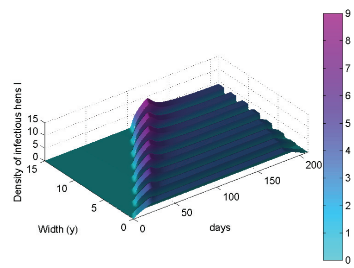
(a) Distribution of susceptible hens at Day 0 in the hen house.



(b) Distribution of susceptible hens at Day 0 along the section of the hen house.



(c) Density of infectious hens at Days 0, 100, and 180 in the hen house.



(d) Evolution of the infectious hens density summed along the x-direction.

FIG. 7.1. *Results of simulations achieved with estimated parameters in Table* 7.1. (a), (b) *Distribution of susceptible hens at Day* 0. (c) *Superimposed infectious hens densities I defined by* (7.3) *at Days* 0, 100, *and* 180*; the epizootic starts at Day* 0 *in the corner located at* (0,0) *and reaches the last row around Day* 100 *as in Figure* 8(a) *in* [51]. (d) *Infectious hens density $\int_0^{30} I(t,x,y)\,dx$ depending on width (y) and time (t) in days; the result is similar to Figure* 8(a) *in* [51].

In this scenario, the hen house is 15 m wide (L_y) and 30 m long (L_x). Moreover, the distribution of the hens in the hen house is not uniform. Indeed the hen house contains 8 rows of cages separated by hen-free intervals of 1 m, the hens density in the cages is uniform and equals 10 hens per m^2. The corresponding initial distribution of the hens density $S_0(y)$ is displayed in Figures 7.1(a) and (b). At Day 0, one hen in the corner is inoculated.

Now notice that the higher the value of the disease transmission rate σ, the sooner the disease will reach the last row at the other side of the hen house. In Figure 8(a) in [51], it took an average time of 100 days for the epizootic to reach this row. By a bisection process we found that for our model, all other parameters being set as above, the corresponding value of σ is approximately 10^{-5} cfu$^{-1}\cdot$Day^{-1}, i.e., it is the lowest value of σ for which the epizootic reaches the last row within 100 days. The result of this simulation is given in Figures 7.1(c) and (d). Notice that the result of this simulation as displayed in Figure 7.1(d) is visually similar to Figure 8(a) in [51] as expected. Finally, in this scenario the corresponding epidemic threshold computed with formula (2.2) is $R_0(S_0) = 5.26$.

7.2. Influence of heterogeneities in the hen density on the speed of propagation. We now perform some simulations of the calibrated model (1.1). We change the dimensions of the simulated hen house by setting its width L_y to 13 m

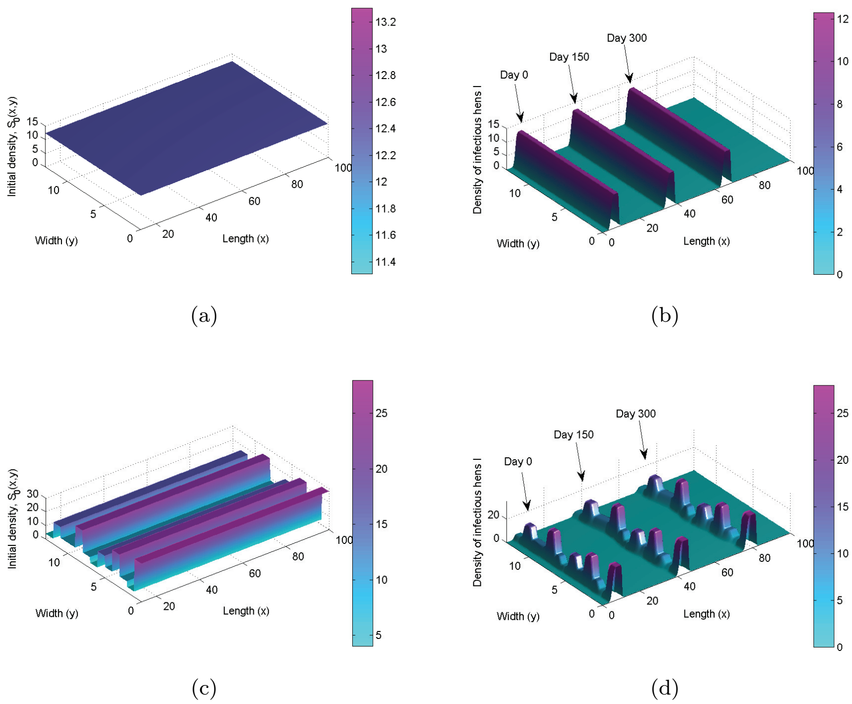


FIG. 7.2. *Results of test case* 1*: For a homogeneous distribution of susceptible hens S_0 at Day* 0 *shown in* (a)*, the corresponding densities of infectious hens I at Days* 0*,* 150*, and* 300 *are superimposed in* (b)*. They take the form of a traveling wave solution that travels in the x-direction. Similarly for the heterogeneous distribution in* (c)*, the corresponding densities of infectious hens are superimposed in* (d)*. The velocity of the traveling wave is higher for the heterogeneous distribution.*

and length L_x to 100 m in order to be closer to the ideal case of an infinite domain $\mathbb{R} \times (0, L_y)$ as assumed for our theoretical results. This is also in good agreement with the dimensions of a real industrial hen house. The duration of the simulations is set to 300 days, which corresponds to the sojourn time of laying hens in a poultry house before being completely removed and changed.

We compare the value of the numerically observed disease propagation speed c along the x-axis for different distributions (along the section) of the hen density $S_0(y)$ in two test cases. Note that in our model the distribution of the hen density along the x-direction is uniform. In what follows, we impose that $\int_0^{13} S_0(y)dy = 160$. This is some kind of normalization assumption motivated by the fact that in the case of a homogeneous distribution the threshold R_0 is proportional to the hen density (see (2.3)).

Test case 1. To illustrate Theorem 2.8, we compare the epidemic thresholds R_0 and wave speeds c obtained for a homogeneous hen distribution S_0 (Figure 7.2(a)) and for a heterogeneous one (Figure 7.2(c)). The results of the simulation at Days 0, 150, and 200 are superimposed in Figure 7.2(b) for the homogeneous distribution, and in Figure 7.2(d) for the heterogeneous one.

For the homogeneous distribution, the speed of propagation is $c \approx 19.80$ cm/day with epidemic thresholds $R_0(S_0) = 11.27$ as given by formula (2.2). For the heterogeneous distribution, c and R_0 are higher, as predicted by

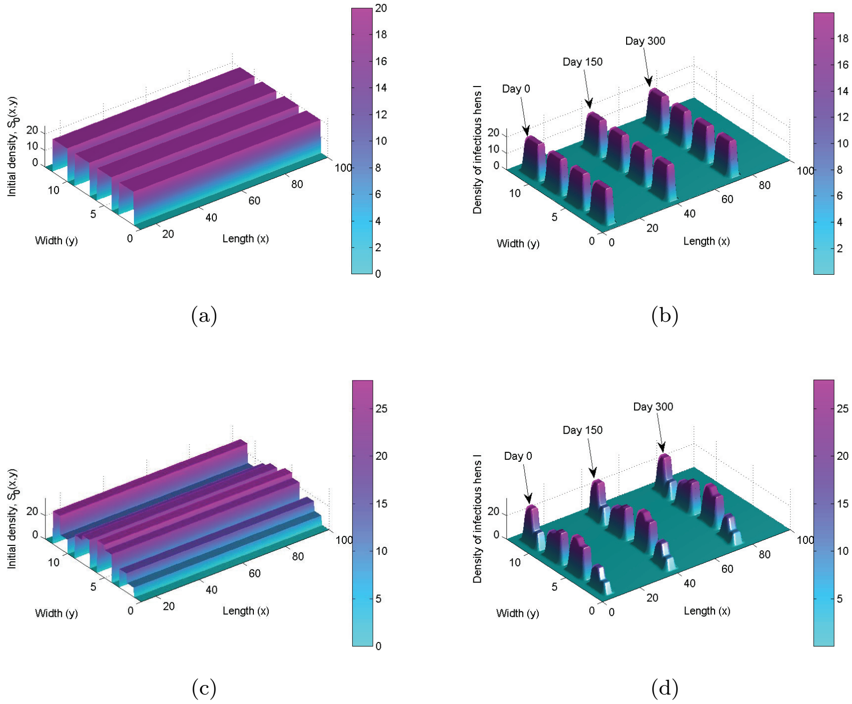


FIG. 7.3. *Results of test case* 2*: For two heterogeneous distributions of susceptible hens* S_0 *at Day* 0 *shown in* (a) *(resp.,* (c)*), the corresponding densities of infectious hens* I *at Days* 0, 150, *and* 300 *are superimposed in* (b) *(resp.,* (d)*). The velocity of the observed traveling wave is higher for the heterogeneous distribution* S_0 *in* (c) *that has a higher maximum than the one in* (a)*.*

Theorem 2.8: the speed of propagation is equal to $c \approx 22.88$ cm/day and $R_0(S_0) = 17.35$

Test case 2. We now use two different initial distributions of hen density in a hen house of 4 rows of contiguous cages as shown in Figures 7.3(a) and (c). The corresponding simulations are displayed in Figures 7.3(b) and (d). Both distributions are heterogeneous since the hen density equals 0 between rows, though the hens density in the cages is uniform for the first one.

We cannot use Theorem 2.8 to predict which distribution yields a higher value of R_0 and c anymore. But according to Theorem 2.10 (slow diffusion asymptotic), which proves that these values are increasing functions of $\|S_0\|_\infty$, the epidemic threshold R_0 and wave speeds c should be higher for the initial distribution (d) (provided the diffusion coefficient D is small enough).

For the first distribution as shown in Figure 7.3(a), the computed speed of propagation is $c \approx 22.00$ cm/day and the epidemic threshold is $R_0(S_0) = 13.02$, and $R_0^\infty(S_0) = 18.32$ is the value given by (2.8) (slow diffusion asymptotic value). For the initialization shown in Figure 7.3(c) the speed is $c \approx 23.47$ cm/day with $R_0(S_0) = 16.04$ and $R_0^\infty(S_0) = 25.65$. These results are in agreement with Theorem 2.10 though there is a strong discrepancy between the values of asymptotic epidemic thresholds $R_0^\infty(S_0)$ and $R_0(S_0)$.

All in all, test cases 1 and 2 confirm the results provided by the mathematical analysis.

8. Concluding remarks. In this article, we formulated a spatial age structured model to describe the spread of *Salmonella* in laying hens in industrial hen houses. Mathematical and numerical analyses of the model have been achieved. Under suitable assumptions, the existence of a traveling wave solution is proved. This existence property is related to the value of the epidemic threshold number R_0. This latter is correlated to the spatial distribution of susceptible hens.

Biologically relevant parameters have been estimated and used to fulfill numerical simulations of the model. These simulations, together with Theorem 2.8, indicate that to decrease or even stop a *Salmonella* epizootic, the best configuration for the hens repartition is the homogeneous one.

In the case of a hen house set with cages in rows, numerical simulations also indicate that the hen density should be uniform in the rows for the propagation and disease risk to be minimal; that is, the number of hens should be the same in all the cages, and in the case of rows with several cages stacked vertically, the number of stacked cages should be kept constant; moreover, hen density peaks should be avoided. This is in agreement with Theorem 2.10, which proves that, considering only the hen density, the disease risk and propagation speed depend only on the maximal value of the hen density inside the hen house. It is worth noting that such conditions are usually observed when hens are reared in cages, while when they are reared on floor, observed densities may vary to a larger extent.

Finally, this study indicates that homogeneous floor rearing seems to be a better housing system with regards to speed of bacterial propagation. Further investigations are needed to evaluate the difference between an on-floor cage system and a cage-free one. However, we suspect that a cage-free system (that induces a local motion of animals) may increase the spreading speed of the disease.

Appendix. Numerical method for solving model (1.1). The method is based on a forward finite difference scheme in time, a centered finite difference scheme in space, and a backward finite difference scheme in age (or equivalently a method of characteristics).

The time interval $(0, T)$ is partitioned into subintervals (t_n, t_{n+1}), with a time step $\delta t = t_{n+1} - t_n$, $n = 0, 1, 2, \ldots, N$.

The trapezoidal rule is used to approximate integral $\int_0^\infty \beta(a) i(t, a, x, y) da$. We assume as in section 7 that there exists a latency period so that $\beta(0) = 0$ and that there exists $A_{\max}$ such that $\beta(a) = 0$ if $a \geq A_{\max}$. The age interval $(0, A_{\max})$ is partitioned into subintervals $(a_\ell, a_{\ell+1})$, with an age step $\delta a = a_{\ell+1} - a_\ell$, $\ell = 0, 1, 2, \ldots, A$; we set $\delta a = \delta t$ for simplicity.

We use a uniform Cartesian grid (x_k, y_j) on the domain $\Sigma = (0, L_x) \times (0, L_y)$, and we let δx and δy be the corresponding space steps.

Let $C^n_{k,j}$, $S^n_{k,j}$ be an approximation of $C(t_n, x_k, y_j)$, $S^n_{k,j} = S(t_n, x_k, y_j)$, respectively, and $i^n_{\ell,k,j}$ an approximation of $i(t_n, a_\ell, x_k, y_j)$. An approximate solution of the model (1.1)–(1.2)–(7.1) is given by

$$\frac{S^{n+1}_{k,j} - S^n_{k,j}}{\delta t} = -\sigma S^{n+1}_{k,j} C^{n+1}_{k,j}, \tag{A.1}$$

$$\frac{i^{n+1}_{\ell,k,j} - i^n_{\ell,k,j}}{\delta t} = -\frac{i^n_{\ell,k,j} - i^n_{\ell-1,k,j}}{\delta a}, \tag{A.2}$$

$$i^{n+1}_{0,k,j} = \sigma S^{n+1}_{k,j} C^{n+1}_{k,j}, \tag{A.3}$$

$$
\begin{aligned}
\frac{C_{k,j}^{n+1} - C_{k,j}^{n}}{\delta t} &= \frac{D}{(\delta x)^2}\left(C_{k+1,j}^{n+1} - 2C_{k,j}^{n+1} + C_{k-1,j}^{n+1}\right) \\
&\quad + \frac{D}{(\delta y)^2}\left(C_{k,j+1}^{n+1} - 2C_{k,j}^{n+1} + C_{k,j-1}^{n+1}\right) \\
&\quad - \alpha C_{k,j}^{n+1} + \delta a \sum_{\ell=1}^{A-1} \beta_\ell i_{\ell,k,j}^{n+1},
\end{aligned} \tag{A.4}
$$

$$
C_{0,j}^{n+1} = C_{1,j}^{n+1}, \quad C_{N_x-1,j}^{n+1} = C_{N_x,j}^{n+1}, \quad C_{k,0}^{n+1} = C_{k,1}^{n+1}, \quad C_{k,N_y-1}^{n+1} = C_{k,N_y}^{n+1}. \tag{A.5}
$$

Now let n be given. Assume $C_{k,j}^n$, $S_{k,j}^n$, and $i_{\ell,k,j}^n$ for all k, j, ℓ have been computed. We first compute $i_{\ell,k,j}^{n+1}$ for all k, j, and $\ell \neq 0$ thanks to (A.2). Then after some algebraic manipulation, one can rewrite (A.4)–(A.5) in the form of a sparse block tridiagonal linear system that yields $C_{k,j}^{n+1}$ for all k, j. We then use (A.1)–(A.2) to find $S_{k,j}^{n+1}$ and $i_{0,k,j}^{n+1}$ for all k, j.

This scheme is implicit in time, which guarantees its stability.

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