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model for hantavirus infection in rodents**

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NUMERICAL SOLUTION OF A SPATIO-TEMPORAL GENDER-STRUCTURED MODEL FOR HANTAVIRUS INFECTION IN RODENTS

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ABSTRACT. The propagation of hantavirus infection in rodents is described by a spatio-temporal susceptible-exposed-infective-recovered (SEIR) compartmental model that distinguishes between male and female subpopulations [L.J.S. Allen, R.K. McCormack and C.B. Jonsson, *Bull. Math. Biol.* **68** (2006), 511–524]. Both subpopulations are assumed to differ in their movement with respect to local variations of the densities of their own and the opposite gender group. Three alternative models for the movement of the male individuals are examined. In particular, in some cases the movement is not only directed by the gradient of a density (as in the standard diffusive case), but also by a non-local convolution of density values as proposed, in another context, in [R.M. Colombo and E. Rossi, *Commun. Math. Sci.*, **13** (2015), 369–400]. An efficient numerical method for the resulting convection-diffusion-reaction system of partial differential equations is proposed. This method involves techniques of weighted essentially non-oscillatory (WENO) reconstructions in combination with implicit-explicit Runge-Kutta (IMEX-RK) methods for time stepping. The numerical results exhibit significant differences in the spatial-temporal behavior predicted by the different models that give rise to future directions of research.

1. **Scope.** Hantavirus (family Bunyaviridae) is a rodent-borne infectious disease of significant concern as it can generate high case fatality rates in the human population [37]. Transmission of hantavirus from infected rodents, the main known reservoir of the virus, to humans, typically occurs via inhalation of aerosols contaminated by virus shed in excreta, saliva, and urine [25]. Risk of infection with hantavirus in the human population is facilitated by crowding conditions and close proximity to rodent populations. Not surprisingly, the total population at risk for hantavirus infection has increased with urbanization rates. In the Americas, hantavirus represents a public health issue in South American countries including Chile [32]. The great majority of hantavirus cases have been reported in China, however. A better understanding of the transmission dynamics of hantavirus in rodent populations has the potential to directly guide interventions strategies aimed at minimizing the number of infections in the human population.

It is the purpose of this contribution to advance a spatio-temporal compartmental model of hantavirus infection in rodents, with a focus on its efficient numerical solution. The model is based on subdividing the total population of rodents into males and females (indices m and f), and for each of both subpopulations a variant of the well-known susceptible-exposed-infective-recovered (SEIR) compartmental model [23] is formulated. The corresponding compartments of male and female individuals are $\mathcal{C}_m := \{S_m, E_m, I_m, R_m\}$ and $\mathcal{C}_f := \{S_f, E_f, I_f, R_f\}$, respectively, and the final model for

$$\mathbf{u} = (u_1, \dots, u_8)^T = (S_m, E_m, I_m, R_m, S_f, E_f, I_f, R_f)^T$$

as a function of position $\mathbf{x} \in \Omega$ and time $t \in \mathcal{T} := [0, T]$ on a bounded domain $\Omega \subset \mathbb{R}^2$ is given by a convection-diffusion reaction system of the type

$$\frac{\partial \mathbf{u}}{\partial t} + \nabla \cdot \mathbf{F}^c(\mathbf{u}) = \mathcal{D} \Delta \mathbf{u} + \mathbf{s}(\mathbf{u}), \quad (1.1)$$

supplied with initial and boundary conditions, where the convective fluxes $\mathbf{F}^c(\mathbf{u})$, the diffusion matrix $\mathcal{D}$ and the vector of reaction terms $\mathbf{s}(\mathbf{u})$ are specified in later parts of the paper. It is proposed to describe the movement of the male individuals in a particular way that depends non-locally on the density $N_f = S_f + E_f + I_f + R_f$ of female individuals, in combination with several alternative local or non-local

dependences on the density $N_m = S_m + E_m + I_m + R_m$ of male individuals. These alternatives give rise to three models that will be discussed in parallel, and that are expressed by the respective choice of $\mathbf{F}^c(\mathbf{u})$. In any case the movement of the male individuals is assumed to depend non-locally on N_f . All variants of (1.1) call for numerical methods that on one hand avoid the severe time step restriction incurred by explicit time discretizations of the diffusion term $\mathcal{D}\Delta\mathbf{u}$, and on the other hand allow the efficient computation of numerical fluxes based on the non-local evaluation of data. As we outline in this paper, the first goal can be achieved by an implicit-explicit (IMEX) discretization in combination with a technique based on Fast Fourier Transform (FFT) to handle the second. The simulator constructed in this way is applied to provide numerical results of several scenarios that allow comparing the model variants.

1.1. Mathematical model. The model for the eight unknowns contained in $\mathcal{C} := \mathcal{C}_m \cup \mathcal{C}_f$, as functions of $\mathbf{x}$ and t , is given as follows:

$$\frac{\partial S_m}{\partial t} + \nabla \cdot F_{S_m}(S_m, N_f, N_m) = \frac{B(N_m, N_f)}{2} - S_m d(N) - S_m(\beta_f I_f + \beta_m I_m), \quad (1.2a)$$

$$\frac{\partial E_m}{\partial t} + \nabla \cdot F_{E_m}(E_m, N_f, N_m) = -E_m d(N) + S_m(\beta_f I_f + \beta_m I_m) - \delta E_m, \quad (1.2b)$$

$$\frac{\partial I_m}{\partial t} + \nabla \cdot F_{I_m}(I_m, N_f, N_m) = \delta E_m - I_m d(N) - \gamma_m I_m, \quad (1.2c)$$

$$\frac{\partial R_m}{\partial t} + \nabla \cdot F_{R_m}(R_m, N_f, N_m) = \gamma_m I_m - R_m d(N), \quad (1.2d)$$

$$\frac{\partial S_f}{\partial t} - \nabla \cdot (\mu_{S_f} \nabla S_f) = \frac{B(N_m, N_f)}{2} - S_f d(N) - S_f(\beta_f I_f + \beta_{m,f} I_m), \quad (1.2e)$$

$$\frac{\partial E_f}{\partial t} - \nabla \cdot (\mu_{E_f} \nabla E_f) = -E_f d(N) + S_f(\beta_f I_f + \beta_{m,f} I_m) - \delta E_f, \quad (1.2f)$$

$$\frac{\partial I_f}{\partial t} - \nabla \cdot (\mu_{I_f} \nabla I_f) = \delta E_f - I_f d(N) - \gamma_f I_f, \quad (1.2g)$$

$$\frac{\partial R_f}{\partial t} - \nabla \cdot (\mu_{R_f} \nabla R_f) = \gamma_f I_f - R_f d(N), \quad (1.2h)$$

where $\nabla \cdot$ denotes the (spatial) divergence operator. The right-hand sides of (1.2) are identical to that of the non-spatial model proposed in [2], i.e., this model, to which we refer as Model 0 for ease of reference, is recovered if all divergence terms on the left-hand sides are set to zero and variables are considered to depend on t only, and the unknowns represent suitably scaled densities. In particular $d(N)$ is the density-dependent death rate, β_f is the contact rate of an infective female with either a susceptible female or a susceptible male, $\beta_{m,f}$ is the contact rate of an infective male with a susceptible female, β_m is the contact rate of an infective male with a susceptible male, δ is the inverse of the average length of the incubation period (assumed to be the same for males and females), and γ_m and γ_f are the inverse of average length of the infectious periods for males and females, respectively. Following [2], we assume a harmonic birth function,

$$B(N_m, N_f) = \frac{2bN_mN_f}{N_m + N_f},$$

where b is the average litter size, and regarding the contact rates and infectious periods, we assume $\beta_m \geq \beta_{m,f} \geq \beta_f$ and $\gamma_f > \gamma_m$. The incubation period is the

same for males and females (namely $1/\delta$), as is the density-dependent death rate $d(N) = a + cN$, where $0 < a < b/2$ and $c > 0$.

The fluxes appearing in the left-hand sides of the full spatio-temporal model (1.2) have two components for the male compartments, and one for the female compartments. Several alternative choices of F_X for the males in compartment $X \in \mathcal{C}_m$ will be considered in parallel and compared. Model 1 is given by (1.2) along with

$$F_X(X, N_f, N_m) = X(\kappa_X \mathbf{V}(N_f) - \mu_X \mathbf{V}(N_m)), \quad (1.3)$$

where $\kappa_X \geq 0$ and $\mu_X \geq 0$ are constants and $\mathbf{v}$ is a non-local velocity function that will be specified below. Model 2 is given by (1.2) in combination with

$$F_X(X, N_f, N_m) = X\varphi(N_m + N_f)(\kappa_X \mathbf{V}(N_f) - \mu_X \mathbf{V}(N_m)), \quad (1.4)$$

where the function φ is given by

$$\varphi(u) = \begin{cases} 1 - u/K & \text{for } 0 \leq u \leq K, \\ 0 & \text{for } u < 0 \text{ or } u > K, \end{cases} \quad (1.5)$$

where K is a maximum value (carrying capacity) of the total density. Finally, we consider Model 3 that is given by

$$F_X(X, N_f, N_m) = X\kappa_X \mathbf{V}(N_f) - \mu_X \nabla X, \quad (1.6)$$

where ∇X is the spatial gradient of X .

The non-local unscaled velocity $\mathbf{V}$ is defined as

$$\mathbf{V}(w) = \frac{\nabla(w * \eta)}{\sqrt{1 + \|\nabla(w * \eta)\|^2}}, \quad (1.7)$$

where η denotes a radial convolution kernel with radius ε , i.e., η is a piecewise smooth function such that $\eta(\mathbf{x}) = \eta(\|\mathbf{x}\|_2)$, $\eta(\mathbf{x}) \geq 0$, $\eta(\mathbf{x}) = 0$ for $\|\mathbf{x}\| > \varepsilon$, and $\int_{\mathbb{R}^2} \eta(\mathbf{x}) d\mathbf{x} = 1$, i.e., for any function w defined on $\Omega \times \mathcal{T}$ and $\mathbf{x} \in \Omega$ such that $B_\varepsilon(\mathbf{x}) := \{\mathbf{y} \in \mathbb{R}^2 : \|\mathbf{y} - \mathbf{x}\| < \varepsilon\} \subset \Omega$, we have

$$(w(\cdot, t) * \eta)(\mathbf{x}) = \int_{B_\varepsilon(\mathbf{x})} w(\mathbf{y}, t) \eta(\mathbf{x} - \mathbf{y}) d\mathbf{y} = \int_{\mathbb{R}^2} w(\mathbf{y}, t) \eta(\mathbf{x} - \mathbf{y}) d\mathbf{y}.$$

(This definition will be modified slightly for points $\mathbf{x}$ with $\text{dist}(\mathbf{x}, \partial\Omega) < \varepsilon$.) It is worth recalling that

$$\nabla(w * \eta) = w * \nabla\eta, \quad (1.8)$$

so that $\mathbf{V}(w)$ indeed depends (non-locally) on w and not on its gradient.

The non-local velocity function (1.7) was introduced recently in a two-species predator-prey model by Colombo and Rossi [17], for which convergence of a numerical scheme was proved by Rossi and Schleper [33]. This velocity function is evaluated at $w = N_f$ in the equations for male individuals, and describes that males are attracted by females since the corresponding biological fluxes $\kappa_C \mathbf{V}(N_f)$, $C \in \mathcal{C}_m$, are directed toward increasing densities of females, while the terms $-\mu_X \nabla X$ describe movement in direction of decreasing densities of individuals of compartment X . The biological movement of females is standard diffusion.

Summarizing, we obtain that the convective fluxes $\mathbf{F}^c(\mathbf{u})$ and the diffusion matrix $\mathcal{D}$ arising in (1.1) are given by the respective expressions

$$\begin{aligned} \mathbf{F}^c(\mathbf{u}) = & (F_{S_m}(S_m, N_f, N_m), F_{E_m}(E_m, N_f, N_m), F_{I_m}(I_m, N_f, N_m), \\ & F_{R_m}(R_m, N_f, N_m), 0, 0, 0, 0)^T, \end{aligned}$$

$$\mathcal{D} = \text{diag}(0, 0, 0, 0, \mu_{S_f}, \mu_{E_f}, \mu_{I_f}, \mu_{R_f}),$$

when the definition of the fluxes is (1.3) (Model 1) or (1.4), (1.5) (Model 2), and

$$\begin{aligned} \mathbf{F}^c(\mathbf{u}) &= (S_m \kappa_{S_m} \mathbf{V}(N_f), E_m \kappa_{E_m} \mathbf{V}(N_f), I_m \kappa_{I_m} \mathbf{V}(N_f), \\ &\quad R_m \kappa_{R_m} \mathbf{V}(N_f), 0, 0, 0, 0)^T, \\ \mathcal{D} &= \text{diag}(\mu_{S_m}, \mu_{E_m}, \mu_{I_m}, \mu_{R_m}, \mu_{S_f}, \mu_{E_f}, \mu_{I_f}, \mu_{R_f}), \end{aligned}$$

for the definition of the fluxes (1.6) (Model 3). In all cases, the vector of reaction terms $\mathbf{s}(\mathbf{u}) = (s_1(\mathbf{u}), \dots, s_8(\mathbf{u}))^T$ is given by the right-hand sides of (1.2), i.e.,

$$s_1(\mathbf{u}) = \frac{B(N_m, N_f)}{2} - S_m d(N) - S_m (\beta_f I_f + \beta_m I_m), \dots, s_8(\mathbf{u}) = \gamma_f I_f - R_f d(N).$$

The system (1.2) is considered on $\Omega \times \mathcal{T}$ together with the initial condition

$$\mathbf{u}(\mathbf{x}, 0) = \mathbf{u}_0(\mathbf{x}), \quad \mathbf{x} \in \Omega, \quad (1.9)$$

where $\mathbf{u}_0$ is a given function, and zero-flux boundary conditions

$$(\mathbf{F}^c(\mathbf{u}) - \mathcal{D} \nabla \mathbf{u}) \cdot \mathbf{n} = \mathbf{0}, \quad \mathbf{x} \in \partial\Omega, \quad t \in (0, T], \quad (1.10)$$

where $\mathbf{n}$ is the unit exterior normal vector to the boundary $\partial\Omega$ of Ω .

1.2. Related work. First of all, we mention that general references to the spatial spread of infectious diseases include [3, 19, 28, 30, 34, 41]. The basic assumption of (1.2), namely that all epidemiological compartments are distributed over the whole spatial domain, is opposed to the alternative metapopulation approach that describes spatial structure through the relations between a number of well-identified sub-populations or “patches” (cf., e.g., [1, 4, 5, 15, 24, 38, 39]).

To put our specific approach further into the proper perspective of literature, assume that $\kappa_C = \kappa_m$ and $\mu_C = \mu_m$ for all $C \in \mathcal{C}_m$ and $\mu_C = \mu_f$ for all $C \in \mathcal{C}_f$. Then, summing (1.2a)–(1.2d) and (1.2e)–(1.2h), respectively, we get the two equations

$$\frac{\partial N_m}{\partial t} + \nabla \cdot (\kappa_m N_m \mathbf{V}(N_f) - \mu_m \nabla N_m) = \frac{B(N_m, N_f)}{2} - N_m d(N_m + N_f), \quad (1.11a)$$

$$\frac{\partial N_f}{\partial t} - \mu_f \Delta N_f = \frac{B(N_m, N_f)}{2} - N_f d(N_m + N_f). \quad (1.11b)$$

This model is similar to a nonlocal predator-prey model recently analyzed by Colombo and Rossi [17]. In fact, their model is precisely recovered if we identify N_m as the density of “predators”, N_f as that of “prey”, set $\kappa_m = 1$ and $\mu_m = 0$, and replace the right-hand sides of (1.11a) and (1.11b) by the respective expressions $(\alpha N_f - \beta) N_m$ and $(\gamma - \delta N_m) N_f$, with positive constants $\alpha, \beta, \gamma, \delta$, of the well-known Lotka-Volterra predator-prey kinetics [13]. Furthermore, a numerical scheme for that model is analyzed in [33]. The scheme proposed in that paper is based on the Lax-Friedrichs scheme for the (hyperbolic) equation (1.11a) for the ease of demonstrating convergence properties; we here employ higher-order weighted essentially non-oscillatory (WENO) reconstructions (initially proposed in [21, 27]) to achieve high-order spatial accuracy.

Furthermore, since IMEX Runge-Kutta (IMEX-RK) schemes play an important role in our approach, we briefly provide some background on these methods. Roughly speaking, an IMEX-RK method for a convection-diffusion-reaction equation of the type (1.1) consists of a Runge-Kutta scheme with an implicit discretization of the diffusive term combined with an explicit one for the convective and

reactive terms. To introduce the main idea, we consider the problem

$$\frac{d\mathbf{v}}{dt} = \Phi^*(\mathbf{v}) + \Phi(\mathbf{v}), \quad (1.12)$$

which is assumed to represent a method-of-lines semi-discretization of (1.1), where $\Phi^*(\mathbf{v})$ and $\Phi(\mathbf{v})$ are spatial discretizations of the convective and reactive terms and of the diffusive term, respectively. Assume, for simplicity, that the spatial mesh width is $h > 0$ in both the x - and y -direction. Then the stability restriction on the time step Δt that explicit schemes impose when applied to (1.12) is very severe (Δt must be proportional to the square h^2 of the grid spacing), due to the presence of $\Phi(\mathbf{v})$. The implicit treatment of both $\Phi^*(\mathbf{v})$ and $\Phi(\mathbf{v})$ would remove any stability restriction on Δt . However, the upwind nonlinear discretization of the convective terms contained in $\Phi^*(\mathbf{v})$ that is needed for stability, makes its implicit treatment extremely involved. This situation becomes even more complicated due to the WENO reconstructions. In fact, after the pioneering work of Crouzeix [18], numerical integrators that deal implicitly with $\Phi(\mathbf{v})$ and explicitly with $\Phi^*(\mathbf{v})$ can be used with a time step restriction dictated by the convective-reactive term alone. These schemes, apart from having been profusely used in convection-diffusion problems and convection problems with stiff reaction terms [6, 20], have been recently used to deal with stiff terms in hyperbolic systems with relaxation (see [9–12, 31]). Finally, we mention that many authors have proposed IMEX-RK schemes for the solution of semidiscretized PDEs [6, 22, 31, 45].

1.3. Outline of the paper. The remainder of this work is organized as follows. In Section 2 we introduce the numerical scheme. We will use the methods of lines to obtain a spatial semi-discretization of (1.2), (1.9), (1.10) in the form of a system of ordinary differential equations (ODEs), to which a time-stepping procedure will be applied to obtain the final numerical scheme. To this end we introduce in Section 2.1 the Cartesian grid and discrete unknowns, and describe in Section 2.2 the discretization of nonlocal terms as in (1.7) that appear in the male convective fluxes. Then, in Section 2.3, we introduce the discretization of the complete convective flux for the male species. This is essentially done by WENO reconstruction. The corresponding discretization for the female species is similar, and is omitted. Next, in Section 2.4 we describe the IMEX-RK time integrators used to solve the system of ODEs that represents the spatial discretization. Section 3 is devoted to the presentation of numerical results. Preliminaries are introduced in Section 3.1, including a definition of the constants arising in the model and of the initial scenarios. To make our results comparable with those of [2] (based on ordinary and stochastic differential equations), we adopt the parameters corresponding to the epizootology of the rice rat and the Bayou virus utilized in that paper. On the other hand, Scenario 1 is based on the hypothesis that the initial population occupies a well-identified subdomain of Ω and therefore the numerical results also address the phenomenon of biological invasion (besides that of the progression of epidemic states), while Scenario 2 aims at studying the effect of a random perturbation of a constant initial state. The corresponding numerical examples are presented in Sections 3.2 and 3.3, respectively. Conclusions are collected in Section 4.

2. Numerical scheme.

2.1. Discretization of local convection and diffusion terms. We take $\Omega = [0, L] \times [0, L]$ and use a Cartesian grid with nodes (x_i, y_j) , $i, j = 1, \dots, M$, with $x_i = y_i = (i - 1/2)h$, $h = L/M$.

We discretize $\nabla \cdot \mathbf{F}^c(\mathbf{u})$ on this grid by weighted essentially non-oscillatory (WENO) finite differences and $\Delta \mathbf{u}$ by the standard second-order scheme with a five-point stencil to get a spatial semi-discretization of (1.1) for an $8 \times M \times M$ -matrix $\mathbf{v}(t)$ of unknown approximations

$$\mathbf{v}_{\ell, i, j}(t) \approx u_{\ell}(x_i, y_j, t), \quad i, j = 1, \dots, M, \quad \ell = 1, \dots, 8$$

given by

$$\mathbf{v}' = -\nabla_h \cdot \tilde{\mathbf{F}}^c(\mathbf{v}) + \mathbf{B}\mathbf{v} + \mathbf{S}(\mathbf{v}), \quad (2.1)$$

to which suitable implicit-explicit Runge-Kutta (IMEX-RK) schemes will be applied for obtaining the final fully-discrete scheme (see Section 2.4). In this equation $\nabla_h \cdot \tilde{\mathbf{F}}^c(\mathbf{v})$ is the discretization of $\nabla \cdot \mathbf{F}^c(\mathbf{u})$, to be defined in Section 2.3, and

$$(\mathbf{B}\mathbf{v})_{\ell, i, j} = \mu_{\ell}(\Delta_h \mathbf{v}_{\ell})_{i, j}, \quad i, j = 1, \dots, M, \quad \ell = 1, \dots, 8 \quad (2.2)$$

is the discretization of the diffusion terms. Notice that we take $\mu_{\ell} = 0$ for $\ell \in \{1, 2, 3, 4\}$ and models (1.3) or (1.4), for these models do not have diffusion for male species. Here we have used the notation $\mathbf{v}_{\ell}$ for the $M \times M$ submatrix given by $(\mathbf{v}_{\ell})_{i, j} = \mathbf{v}_{\ell, i, j}$ and Δ_h for the standard two-dimensional Laplacian operator with Neumann boundary conditions. Furthermore, $\mathbf{S}(\mathbf{v})$ is the $8 \times M \times M$ -matrix with components

$$\mathbf{S}(\mathbf{v})_{\ell, i, j} = s_{\ell}(\mathbf{v}_{\ell, i, j}), \quad i, j = 1, \dots, M, \quad \ell = 1, \dots, 8,$$

with corresponding submatrices $\mathbf{S}_{\ell}(\mathbf{v})$, given by

$$\mathbf{S}_{\ell}(\mathbf{v})_{i, j} = s_{\ell}(\mathbf{v}_{\ell, i, j}). \quad (2.3)$$

We explain the discretization of the convective term appearing in (2.1) in the next two subsections.

2.2. Discretization of the convolutions. We will use the following identity for the implementation that arises from (1.7) if we take into account (1.8):

$$\mathbf{V}(w) = \frac{w * \boldsymbol{\nu}}{\sqrt{1 + \|w * \boldsymbol{\nu}\|^2}}, \quad \boldsymbol{\nu} = \left(\frac{\partial \eta}{\partial x}, \frac{\partial \eta}{\partial y} \right). \quad (2.4)$$

The convolutions $w * \chi$, $\chi = \partial \eta / \partial x$ or $\chi = \partial \eta / \partial y$, namely

$$(w * \chi)(\mathbf{x}) = \int_{B_{\varepsilon}(0)} w(\mathbf{x} - \mathbf{y}) \chi(\mathbf{y}) \, d\mathbf{y},$$

are calculated approximately on the discrete grid via a composite Newton-Cotes quadrature formula, such as the composite Simpson rule.

Since $B_{\varepsilon}(0) \subseteq [-rh, rh]^2$, $r = \lceil \varepsilon/h \rceil < M$, and considering that, according to boundary conditions, w is extended to the exterior of Ω by reflection, e.g. by setting $w(-x, y) = w(x, y)$, $(x, y) \in \Omega$, we obtain

$$\begin{aligned} (w * \chi)(x_i, y_j) &= \int_{-rh}^{rh} \int_{-rh}^{rh} w(x_i - x, y_j - y) \chi(x, y) \, dx \, dy \\ &\approx h^2 \sum_{p=-r}^r \sum_{q=-r}^r \alpha_p \alpha_q w(x_i - x_p, y_j - y_q) \chi(x_p, y_q), \end{aligned}$$

where α_p and α_q are the coefficients in the quadrature rule (e.g., for the composite Simpson rule, $\alpha = (1, 4, 2, 4, \dots, 2, 4, 1)$). This can be written as

$$(w * \chi)(x_i, y_j) \approx \sum_{p=-r}^r \sum_{q=-r}^r \beta_{p,q} w(x_{i-p}, y_{j-q}), \quad \beta_{p,q} = h^2 \alpha_p \alpha_q \chi(x_p, y_q) \quad (2.5)$$

The accuracy order of this approximation is given by that of the quadrature rule, e.g., it is fourth-order accurate for the composite Simpson rule. Consequently, the approximation (2.8) for $\mathbf{W} = (w_{i,j}) \in \mathbb{R}^{M \times M}$, $w_{i,j} \approx w(x_i, y_j)$, is given by

$$(w * \chi)(x_i, y_j) \approx (\mathbf{W} *_{\mathbf{h}} \beta)_{i,j} := \sum_{p=-r}^r \sum_{q=-r}^r \beta_{p,q} w_{[i-p]_M, [j-q]_M}, \quad (2.6)$$

where we define

$$[i]_M := \begin{cases} -i + 1 & \text{for } -r + 1 \leq i \leq 0, \\ i & \text{for } 1 \leq i \leq M, \\ 2M + 1 - i & \text{for } M + 1 \leq i \leq M + r. \end{cases}$$

The discrete approximation of $\mathbf{V}(w)$ in (2.4) obtained from the approximation $\mathbf{W} \approx w$ is given by

$$\mathbf{V}_h(\mathbf{W}) = \frac{\mathbf{W} *_{\mathbf{h}} \boldsymbol{\nu}}{\sqrt{1 + \|\mathbf{W} *_{\mathbf{h}} \boldsymbol{\nu}\|^2}}, \quad \boldsymbol{\nu} = \left(\frac{\partial \eta}{\partial x}, \frac{\partial \eta}{\partial y} \right).$$

Since $r \approx \varepsilon/h = \varepsilon M/L$, the computational cost of this discrete convolution is $M^2(2r+1)^2 \approx 4\varepsilon^2 M^4/L^2$, which can be very high for large M . This cost can be substantially reduced to $\mathcal{O}(M^2 \log M)$ by performing a convolution with periodic data by Fast Fourier Transforms (FFTs) (see [26, 36]). To achieve this goal, we define from $\mathbf{W} = (w_{i,j}) \in \mathbb{R}^{M \times M}$ a matrix $\tilde{\mathbf{W}} = (\tilde{w}_{i,j}) \in \mathbb{R}^{2M \times 2M}$ such that

$$\tilde{w}_{i,j} = w_{[i]_M, [j]_M}, \quad i, j = 1, \dots, 2M$$

and use the notation $[i]_{2M}' = \text{mod}(i-1, 2M) + 1$, i.e., $[i]_{2M}' = i + 2kM$, with k being the integer such that $1 \leq [i]_{2M}' \leq 2M$. With this notation it is readily checked that

$$w_{[i]_M, [j]_M} = \tilde{w}_{[i]_{2M}', [j]_{2M}'}, \quad i, j = -r + 1, \dots, M + r.$$

Therefore (2.6) for $i, j = 1, \dots, M$ can be rewritten as

$$(\mathbf{W} *_{\mathbf{h}} \beta)_{i,j} = \sum_{p=-r}^r \sum_{q=-r}^r \beta_{p,q} \tilde{w}_{[i-p]_{2M}', [j-q]_{2M}'}. \quad (2.7)$$

The convolution on the right-hand side of (2.7) can be performed by FFTs applied to the $(2M) \times (2M)$ matrix $\tilde{\mathbf{W}}$. To save further computational costs, the FFT of the kernel $\beta_{p,q}$ is performed only once, so each convolution entails two two-dimensional FFT of $(2M) \times (2M)$ matrices and a product of $4M^2$ numbers, with an overall computational cost of $\mathcal{O}(M^2 \log M)$.

2.3. Discretization of the convective term. The convective flux for the ℓ (female) species, $\ell \in \{5, 6, 7, 8\}$, is zero and the convective flux for the ℓ (male) species, $\ell \in \{1, 2, 3, 4\}$, in e.g., model (1.3) is given by

$$\mathbf{F}_{\ell}^c(\mathbf{u}) = \mathbf{u}_{\ell} (\kappa_{\ell} \mathbf{V}(u_5 + u_6 + u_7 + u_8) - \mu_{\ell} \mathbf{V}(u_1 + u_2 + u_3 + u_4)).$$

To discretize its divergence $\nabla \cdot \mathbf{F}_\ell^c(\mathbf{u})$, for the approximation $\mathbf{v}$, we first approximate the convolution terms as expounded in Section 2.2 to obtain

$$\tilde{\mathbf{F}}_\ell^c(\mathbf{v})_{i,j} = \mathbf{v}_{\ell,i,j} (\kappa_\ell \mathbf{V}_h (v_5 + v_6 + v_7 + v_8)_{i,j} - \mu_\ell \mathbf{V}_h (v_1 + v_2 + v_3 + v_4)_{i,j}) \in \mathbb{R}^2.$$

Similar arguments are carried out for the other models (1.4) and (1.6).

We introduce the following notation

$$(f_{i,j}^x, f_{i,j}^y) := \tilde{\mathbf{F}}_\ell^c(\mathbf{v})_{i,j},$$

where we have dropped the ℓ index for obtaining clearer expressions.

Our purpose is to use a fifth-order WENO finite difference discretization [21, 27, 35] of $\nabla \cdot \mathbf{F}_\ell^c(\mathbf{u})$ for which

$$\nabla \cdot \mathbf{F}_\ell^c(\mathbf{u})(x_i, y_j) \approx \nabla_h \cdot \tilde{\mathbf{F}}^c(\mathbf{v})_{\ell,i,j} := \frac{\hat{f}_{i+1/2,j}^x - \hat{f}_{i-1/2,j}^x}{h} + \frac{\hat{f}_{i,j+1/2}^y - \hat{f}_{i,j-1/2}^y}{h}, \quad (2.8)$$

for suitable numerical fluxes $\hat{f}_{i+1/2,j}^x, \hat{f}_{i,j+1/2}^y$ obtained by WENO reconstructions of split fluxes. For the numerical flux in the x -direction, the Lax-Friedrichs-type flux splitting $f^{x,\pm}$ is given by:

$$f_{i,j}^{x,\pm} = \frac{1}{2} (f_{i,j}^x \pm \alpha^x v_{\ell,i,j}), \quad \alpha^x = \max_{i,j} |\mathbf{V}_h^x(\mathbf{v})_{i,j}|.$$

Likewise, the numerical flux $\hat{f}_{i,j+1/2}^y$ is obtained by WENO reconstructions of split fluxes given by

$$f_{i,j}^{y,\pm} = \frac{1}{2} (f_{i,j}^y \pm \alpha^y v_{\ell,i,j}), \quad \alpha^y = \max_{i,j} |\mathbf{V}_h^y(\mathbf{v})_{i,j}|.$$

If $\mathcal{R}^\pm$ denotes fifth-order WENO upwind biased reconstructions, then

$$\begin{aligned} \hat{f}_{i+1/2,j}^x &= \mathcal{R}^+(f_{i-2:i+2,j}^{x,+}) + \mathcal{R}^-(f_{i-1:i+3,j}^{x,-}), \\ \hat{f}_{i,j+1/2}^y &= \mathcal{R}^+(f_{i,j-2:j+2}^{y,+}) + \mathcal{R}^-(f_{i,j-1:j+3}^{y,-}), \end{aligned}$$

where we have used matlab-type notation for submatrices.

2.4. Implicit-Explicit Runge-Kutta schemes. We will use IMEX-RK integrators for ODEs, for which only the diffusion term will be treated implicitly, so we rewrite (2.1) as (1.12), where

$$\Phi^*(\mathbf{v}) := -\nabla_h \cdot \tilde{\mathbf{F}}^c(\mathbf{v}) + \mathbf{S}(\mathbf{v}), \quad \Phi(\mathbf{v}) := \mathbf{B}\mathbf{v}. \quad (2.9)$$

For the diffusive part $\Phi(\mathbf{v})$ we utilize an implicit s -stage diagonally implicit (DIRK) scheme with coefficients $\mathbf{A} \in \mathbb{R}^{s \times s}$, $\mathbf{b}, \mathbf{c} \in \mathbb{R}^s$, in the common Butcher notation, where $\mathbf{A} = (a_{ij})$ with $a_{ij} = 0$ for $j > i$. For the term $\Phi^*(\mathbf{v})$ containing the convective and reactive parts we employ an s -stage explicit scheme with coefficients $\hat{\mathbf{A}} \in \mathbb{R}^{s \times s}$, $\hat{\mathbf{b}}, \hat{\mathbf{c}} \in \mathbb{R}^s$ and $\hat{\mathbf{A}} = (\hat{a}_{ij})$ with $\hat{a}_{ij} = 0$ for $j \geq i$. We will denote the corresponding Butcher arrays by

$$\mathbf{D} := \left. \begin{array}{c} \mathbf{c} \\ \mathbf{A} \\ \mathbf{b}^T \end{array} \right|, \quad \hat{\mathbf{D}} := \left. \begin{array}{c} \hat{\mathbf{c}} \\ \hat{\mathbf{A}} \\ \hat{\mathbf{b}}^T \end{array} \right|.$$

In our simulations, we limit ourselves to the second-order IMEX-RK scheme H-
DIRK2(2,2,2) that corresponds to

$$D = \frac{1/2 \mid 1/2 \quad 0}{1/2 \mid 0 \quad 1/2}, \quad \hat{D} = \frac{0 \mid 0 \quad 0}{1 \mid 1 \quad 0}.$$

Alternative choices are provided and discussed in [8, 9, 31]. If applied to the equation (1.12), then the IMEX-RK scheme gives rise to the following algorithm (see [31]).

Algorithm 2.1.

Input: approximate solution vector $\mathbf{v}^n$ of (1.12) for $t = t^n$

for $p = 1, \dots, s$

compute the stage values:

$$\hat{\mathbf{v}}^{(p)} \leftarrow \mathbf{v}^n + \Delta t \sum_{j=1}^{p-1} \hat{a}_{pj} \mathbf{K}_j, \quad \bar{\mathbf{v}}^{(p)} \leftarrow \mathbf{v}^n + \Delta t \sum_{j=1}^{p-1} a_{pj} \mathbf{K}_j$$

solve for $\mathbf{K}_p$ the linear system

$$\mathbf{K}_p = \Phi^*(\hat{\mathbf{v}}^{(p)}) + \Phi(\bar{\mathbf{v}}^{(p)} + \Delta t a_{pp} \mathbf{K}_p) \quad (2.10)$$

end

$$\mathbf{v}^{n+1} \leftarrow \mathbf{v}^n + \Delta t \sum_{j=1}^s b_j \mathbf{K}_j$$

Output: approximate solution vector $\mathbf{v}^{n+1}$ of (1.12) for $t = t^{n+1} = t^n + \Delta t$.

To solve the linear equation (2.10) that arises in Algorithm 2.1 for $\mathbf{K}_p$, in view of (2.9), we rewrite it as

$$(\mathbf{I} - \Delta t a_{pp} \mathbf{B}) \mathbf{K}_p = \mathbf{b}^{(p)}, \quad \mathbf{b}^{(p)} := \Phi^*(\hat{\mathbf{v}}^{(p)}) + \mathbf{B} \bar{\mathbf{v}}^{(p)}, \quad (2.11)$$

where $\mathbf{I}$ denotes the identity operator for $8 \times M \times M$ matrices. From the definition of the matrix $\mathbf{B}$ in (2.2) and from the definition of Φ^* in (2.9), if we equate the ℓ submatrices along the first dimension of both sides of (2.11) we get

$$\begin{aligned} & (\mathbf{I}_{M \times M} - \Delta t a_{pp} \mu_\ell \mathbf{\Delta}_h) (\mathbf{K}_p)_\ell \\ &= -\nabla_h \cdot \tilde{\mathbf{F}}_\ell^c(\hat{\mathbf{v}}^{(p)}) + \mathbf{S}_\ell(\hat{\mathbf{v}}^{(p)}) + \mu_\ell \mathbf{\Delta}_h \bar{\mathbf{v}}_\ell^{(p)}, \quad \ell = 1, \dots, 8, \end{aligned} \quad (2.12)$$

where $\mathbf{I}_{M \times M}$ is the identity operator on $M \times M$ matrices and, e.g., $(\mathbf{K}_p)_\ell$ is the ℓ submatrix of $\mathbf{K}_p$ along the first dimension, i.e., $((\mathbf{K}_p)_\ell)_{i,j} = (\mathbf{K}_p)_{\ell,i,j}$. Some remarks are due here to detail the final implementation: for $\ell = 1, \dots, 8$, the right hand side of (2.12) is computed from (2.3), (2.2) and (2.8), taking into account that

$$\nabla_h \cdot \tilde{\mathbf{F}}_\ell^c(\hat{\mathbf{v}}^{(p)}) = 0 \quad \text{for } \ell \in \{5, 6, 7, 8\}$$

(i.e., there is no convection in the models for females); if $\mu_\ell = 0$ (for $\ell \in \{1, 2, 3, 4\}$ and models (1.3) and (1.4) there is no diffusion term for males), then

$$(\mathbf{K}_p)_\ell = -(\nabla_h \cdot \tilde{\mathbf{F}}_\ell^c(\hat{\mathbf{v}}^{(p)}))_\ell + \mathbf{S}_\ell(\mathbf{v}),$$

otherwise the solution of (2.12) is performed by Fast Cosine Transforms (due to boundary conditions), which entails a nearly optimal computational cost of $\mathcal{O}(M^2 \log M)$.

3. Numerical examples.

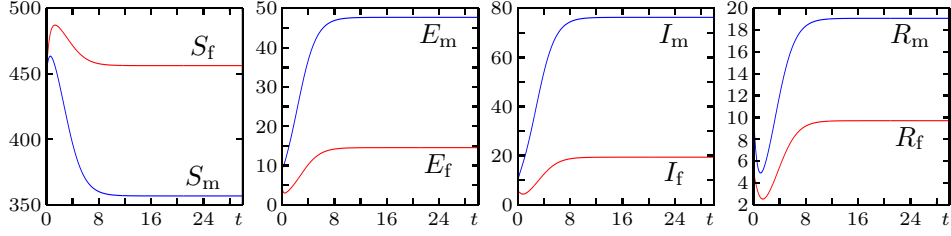


FIGURE 1. Numerical solution of the ODE version of (1.2), Model 0, for the initial data (3.1).

3.1. Preliminaries. According to [2], we assume that two months (60 days) is the basic time unit, $\delta = 4$ ($1/\delta = 15$ days), $b = 4$ (average litter size), $\beta_m = 5\beta_f$, and $\beta_{m,f} = \beta_f$. Moreover, the infectious period for males is assumed to be twice that of females ($1/\gamma_m = 2/\gamma_f$), and the carrying capacity is $K = 1000$ animals. Furthermore, we set $\beta_m = 0.01$, $\gamma_m = 0.5$, $a = 0.01$ and $c = 1.99 \times 10^{-3}$. For these values, the next-generation-matrix method [40] employed in [2] yields a basic reproductive ratio $\mathcal{R}_0 = 1.38$.

We wish to present numerical solutions of the versions of the spatio-temporal model, Models 1 to 3, that can be compared with the example simulated in [2] (that is, by Model 0), and that corresponds to

$$(S_m, E_m, I_m, R_m, S_f, E_f, I_f, R_f)(0) = (450, 10, 10, 10, 450, 5, 5, 5) =: \mathbf{U}_0^T. \quad (3.1)$$

(Figure 1 shows the solution of Model 0 for this case.) To this end, we assume that the spatial domain is $\Omega = [0, 1]^2$ (i.e., $L = 1$ in a scale not specified) and that $K = 1000$ is the maximum density feasible on a unit square. For the simulation, we consider Scenario 1, which corresponds to identifying a subdomain $\Omega_0 \subseteq \Omega$ with $\Omega_0 = \{(x, y) \in \Omega : |x - 0.5| + |y - 0.5| \leq 0.2\}$ in which the initial population is uniformly distributed and setting

$$\mathbf{u}(\mathbf{x}, 0) = \chi_{\Omega_0}(\mathbf{x}) \mathbf{U}_0, \quad \text{where} \quad \chi_{\Omega_0}(\mathbf{x}) = \begin{cases} 1 & \text{if } \mathbf{x} \in \Omega_0, \\ 0 & \text{otherwise,} \end{cases}$$

and alternatively Scenario 2, in which we stipulate a “random” distribution by setting

$$\mathbf{u}(\mathbf{x}, 0) = \frac{1}{|\Omega|} (1 + r(\mathbf{x})) \mathbf{U}_0, \quad \text{where} \quad \int_{\Omega} r(\mathbf{x}) d\mathbf{x} = 0 \quad (3.2)$$

and r is a given oscillatory function assuming values in $(-1, 1)$. (The idea is not to impose any initial “pattern” in Scenario 2.)

A total number of six cases is considered by combining Scenarios 1 and 2 with Models 1, 2 and 3. We always choose $\mu_X = 0.05$ for all species X , $\kappa_X = 0.1$ and $h = 1/200$. Furthermore, we wish to compare the numerical results with the predictions made by the non-spatial ODE model, Model 0 (Figure 1). To this end we determine for each compartment $X \in \mathcal{C}$ and time instants $t^n = n\Delta t$ the following quantity

$$\mathcal{I}(X) = \mathcal{I}(X, t^n) := \frac{1}{h^2} \sum_{i,j=1}^N X_{i,j}^n \approx \int_{\Omega} X(\mathbf{x}, t^n) d\mathbf{x}. \quad (3.3)$$

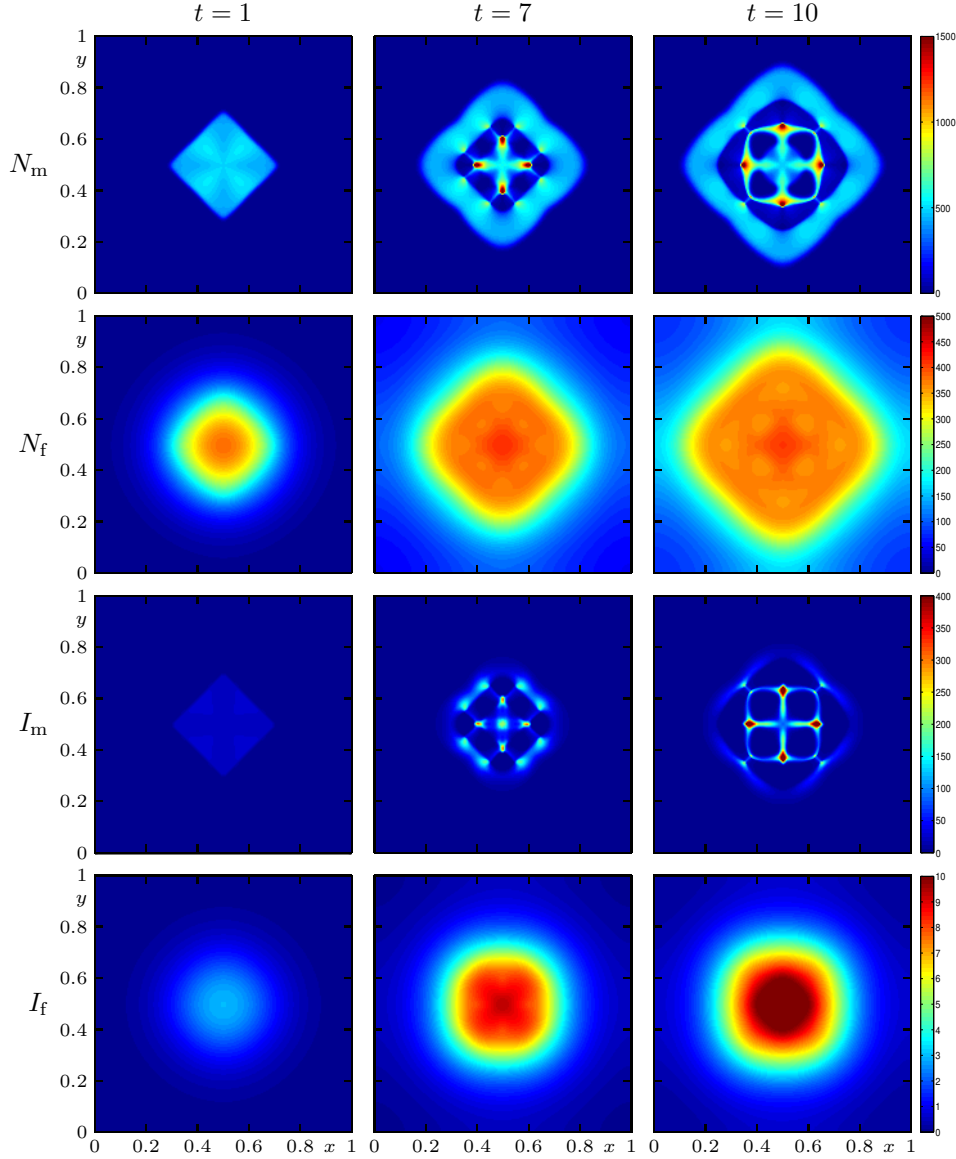


FIGURE 2. Case 1 (Model 1, Scenario 1): numerical solution for N_m , N_f , I_m and I_f at the indicated times.

3.2. Cases 1 to 3: simulations with a structured initial datum. In Figures 2 to 4 we show the numerical solution for N_m , N_f , I_m and I_f , in each case at three different times, for Cases 1 to 3 that arise for Scenario 1 with Model 1, Model 2 with $K = 1000$, and Model 3. First of all, we observe that according to the results for N_m and I_m , within Models 1 and 2 the male individuals keep confined to a growing but sharply limited region, with zero values outside that region. Model 3, with its linear diffusive term $-\mu_X \nabla X$ for $X \in \mathcal{C}_m$ (instead of the expressions $-\mu_X X \mathbf{V}(N_m)$ or $-\mu_X X \varphi(N_m + N_f) \mathbf{V}(N_m)$ in Models 1 or 2), produces a solution that fills the

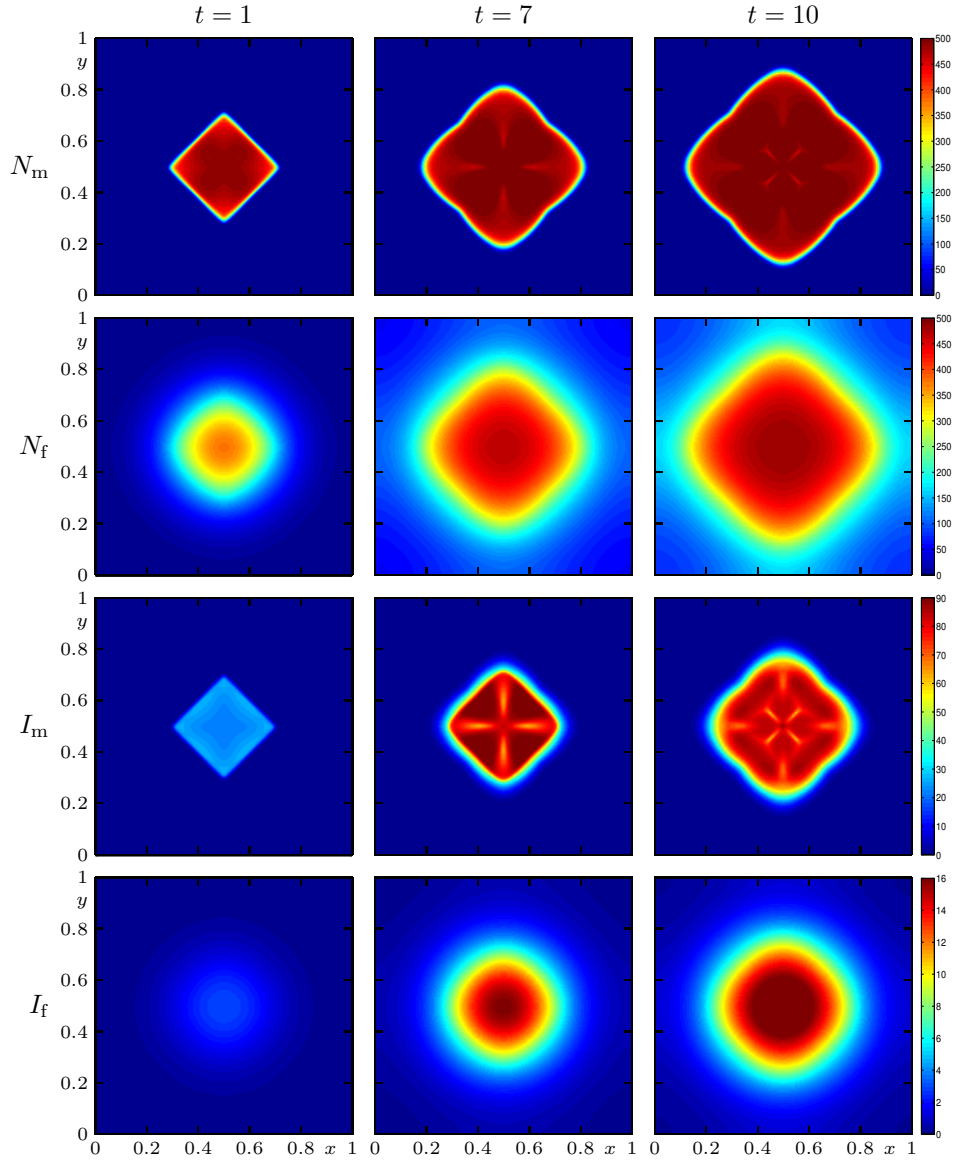


FIGURE 3. Case 2 (Model 2 with $K = 1000$, Scenario 1): numerical solution for N_m , N_f , I_m and I_f at the indicated times.

entire domain. Numerical results obtained for larger times than those shown in Figure 4 indicate that the solutions of all variables become constant on the entire computational domain, and the integral quantities assume a stationary state similar (but not identical) to that of Model 0 (see Figure 1). Furthermore, comparing the results between Models 1 and Models 2 (Figures 2 and 3), we observe that Model 1 gives rise to a distinct spatial structure, including regions that are nearly void of males combined with “peaks” of the solution where $N_m \approx 1500$. Clearly, this feature is expected since Model 1 has no mechanism that would limit the growth of N_m .

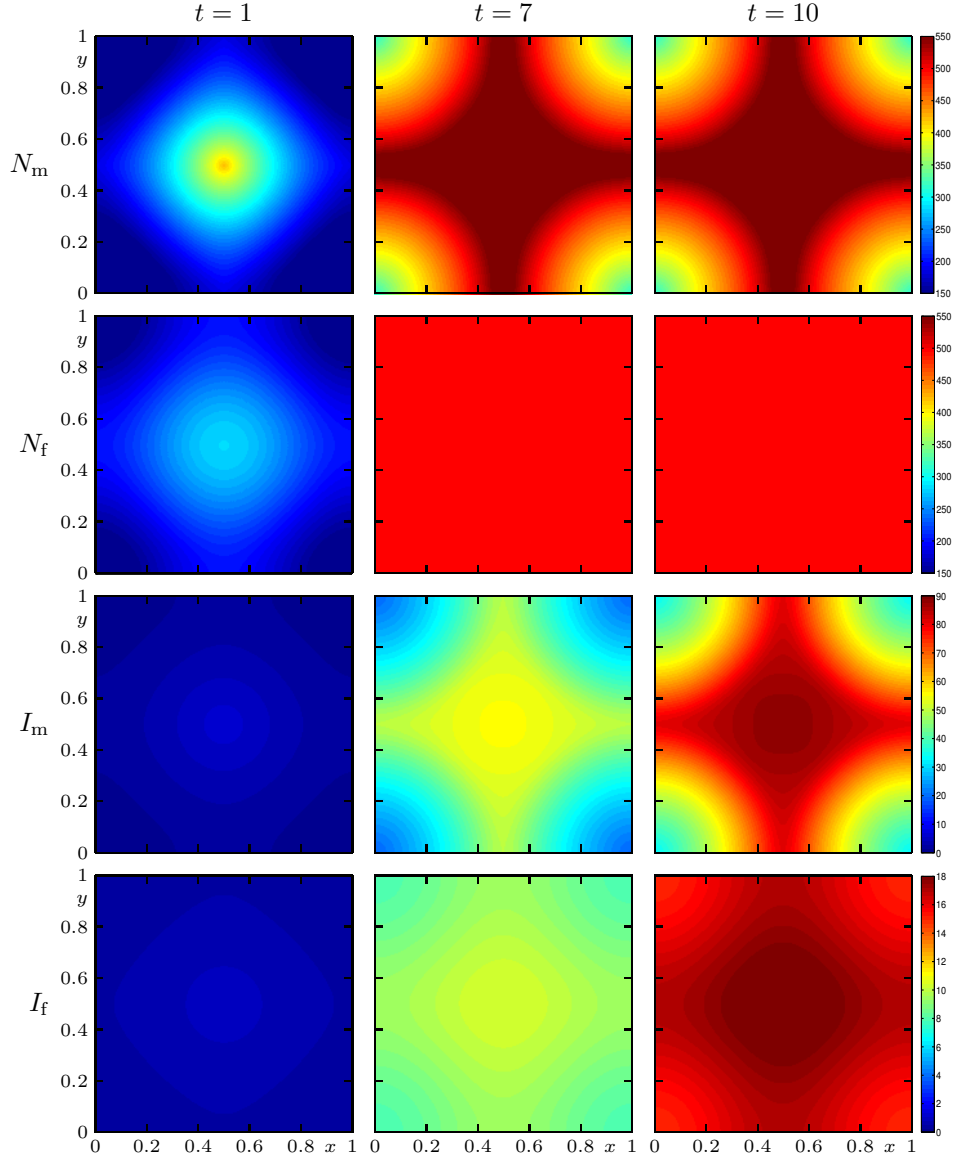


FIGURE 4. Case 3 (Model 3, Scenario 1): numerical solution for N_m , N_f , I_m and I_f at the indicated times.

This is in marked contrast to the results for N_m produced by Model 2 shown in Figures 3, where we observe that N_m does not exceed a value of about 500, and stays close to that value within a region of approximately the same shape as for Model 1. A similar observation is true for the compartment I_m : Model 1 (Figure 2) predicts a structure with “peaks” that roughly mirrors that of N_m , while Model 2 (Figure 3) predicts a more uniform distribution (with I_m assuming values between 70 and 90) in the interior of the domain. Furthermore, we recall that for all models the flux for the female compartments is always given by $-\mu_X \nabla X$ for $X \in \mathcal{C}_f$, so

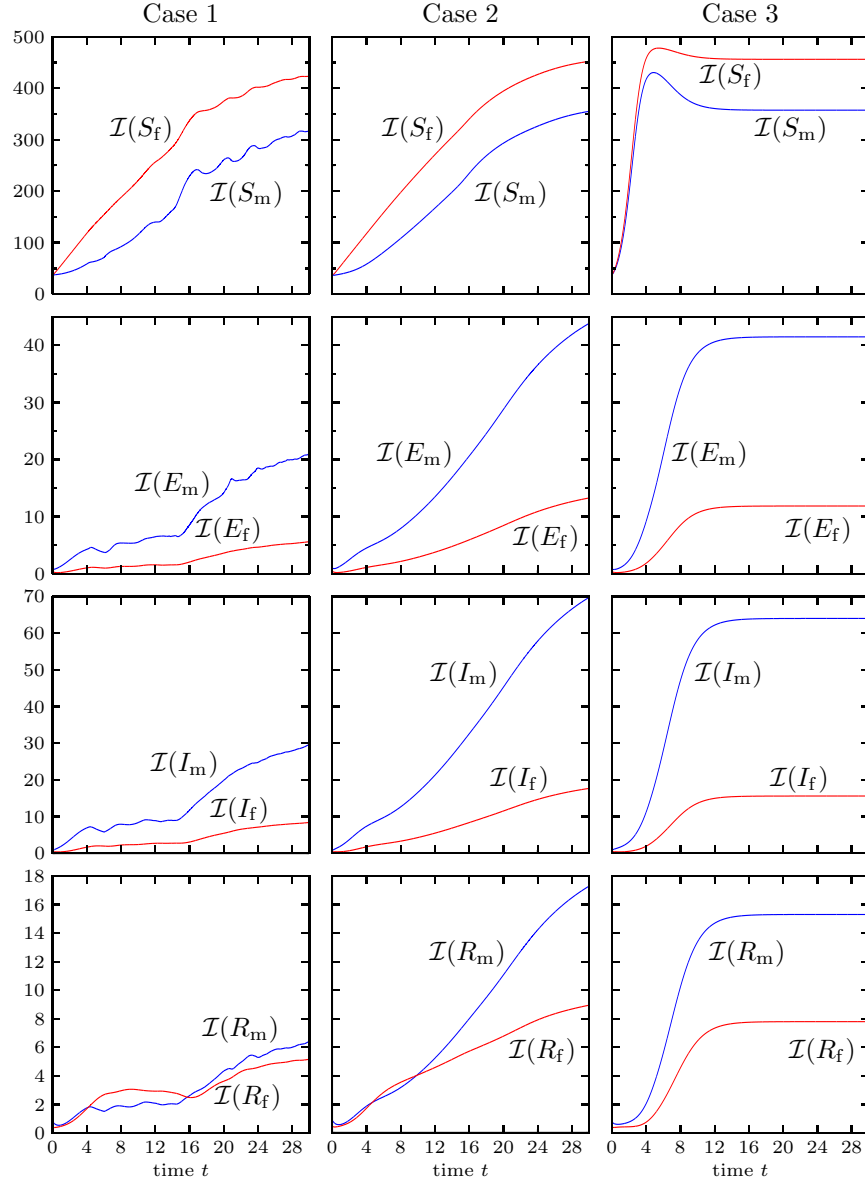


FIGURE 5. Cases 1–3: integral quantities $\mathcal{I}(X)$ defined by (3.3) for each compartment obtained by evaluating numerical solutions.

differences in solution behavior of the female individuals are exclusively due to those in describing the male behavior. In general, this diffusive behavior tends to produce less sharp, smooth spatial structures.

Finally, Figure 5 indicates that Models 1, 2 and 3 lead to quite different numerical results in terms of the integrated quantities (3.3). We commented above that the results of Model 3 are similar to those of Model 0. On the other hand, while Models 1 and 2 produce integral results whose order of magnitude for each compartment is similar to that of Model 3, it can be noted that no stationary state is attained at

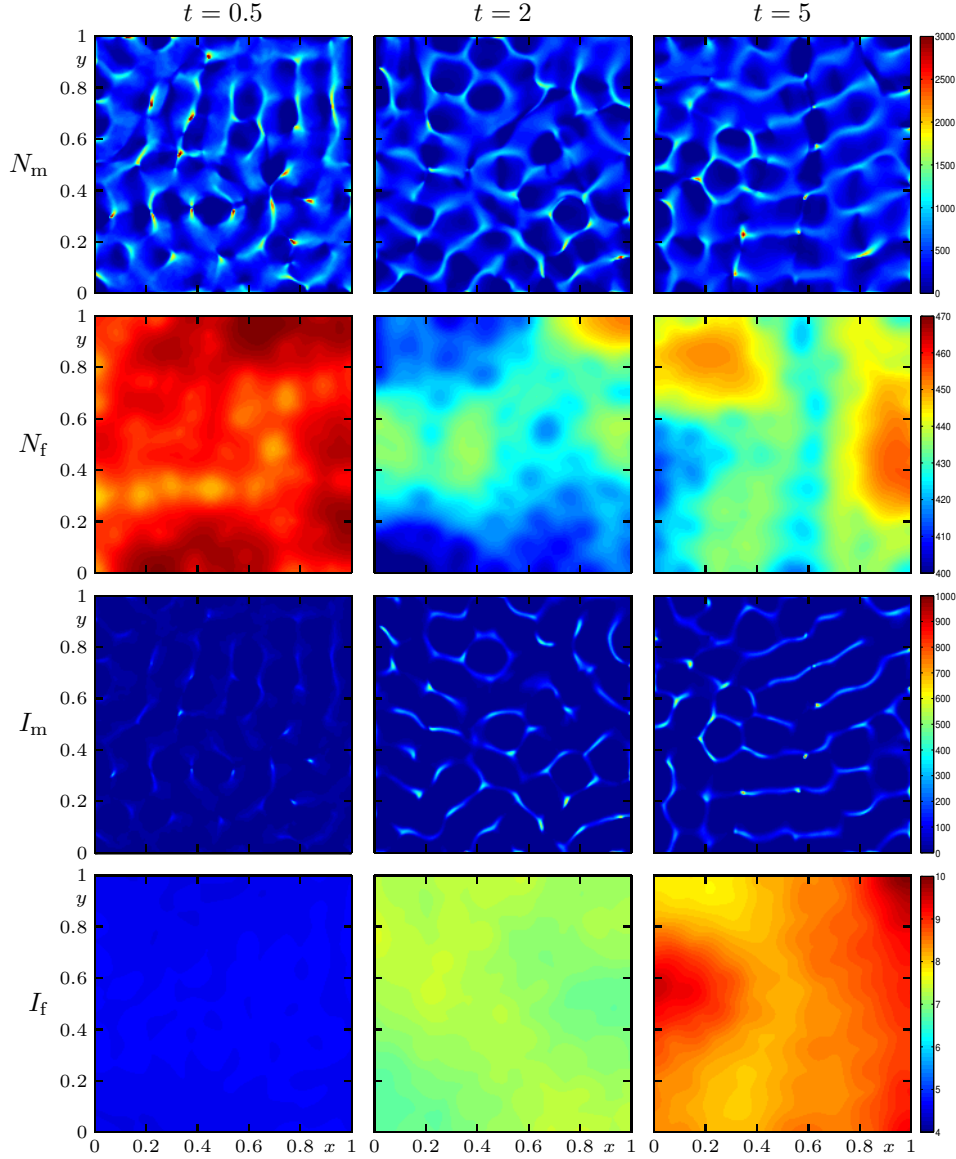


FIGURE 6. Case 4 (Model 1, Scenario 2): numerical solution for N_m , N_f , I_m and I_f at the indicated times.

$t = 30$; as the discussion of Cases 4 to 6, and in particular comparing Figures 5 and 9 show, this is a consequence of the respective model structure in combination with the choice of initial data. In any case, it is calling to attention that while Models 2 and 3 predict a smooth variation of the integrated quantity in time, the curves generated by Model 1 are somewhat oscillatory. This behavior is consistent with our observation that Model 1 does not only generate a spatial solution structure with strong variations, “peaks” and sharp gradients, but also produces rapid transitions

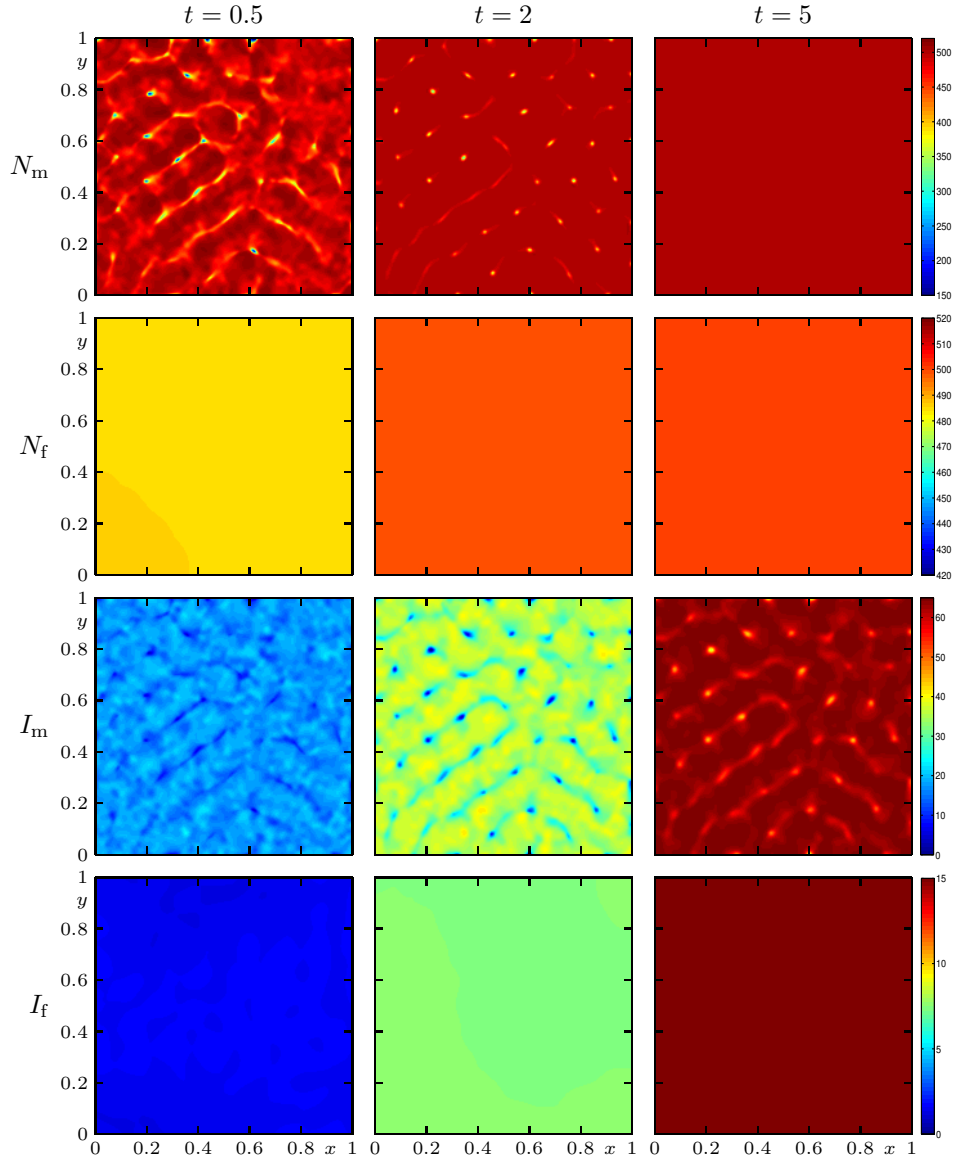


FIGURE 7. Case 5 (Model 2 with $K = 1000$, Scenario 2): numerical solution for N_m , N_f , I_m and I_f at the indicated times.

within time. This unsteady and unstable behavior is due to the strong competence of advective and repulsive mechanisms inherent in the definition (1.3).

3.3. Cases 4 to 6: simulations with a structured initial datum. Figures 6 to 9 provide numerical solutions for Scenario 2. The “random” initial datum (3.2) has been chosen to test whether small perturbations would give rise to large-scale regular structures akin to the well-known mechanism of pattern formation (cf., e.g., [28, 30]), or rather, the small fluctuations in the initial datum would simply be smoothed out. Figure 6, corresponding to Model 1, illustrates that male individuals

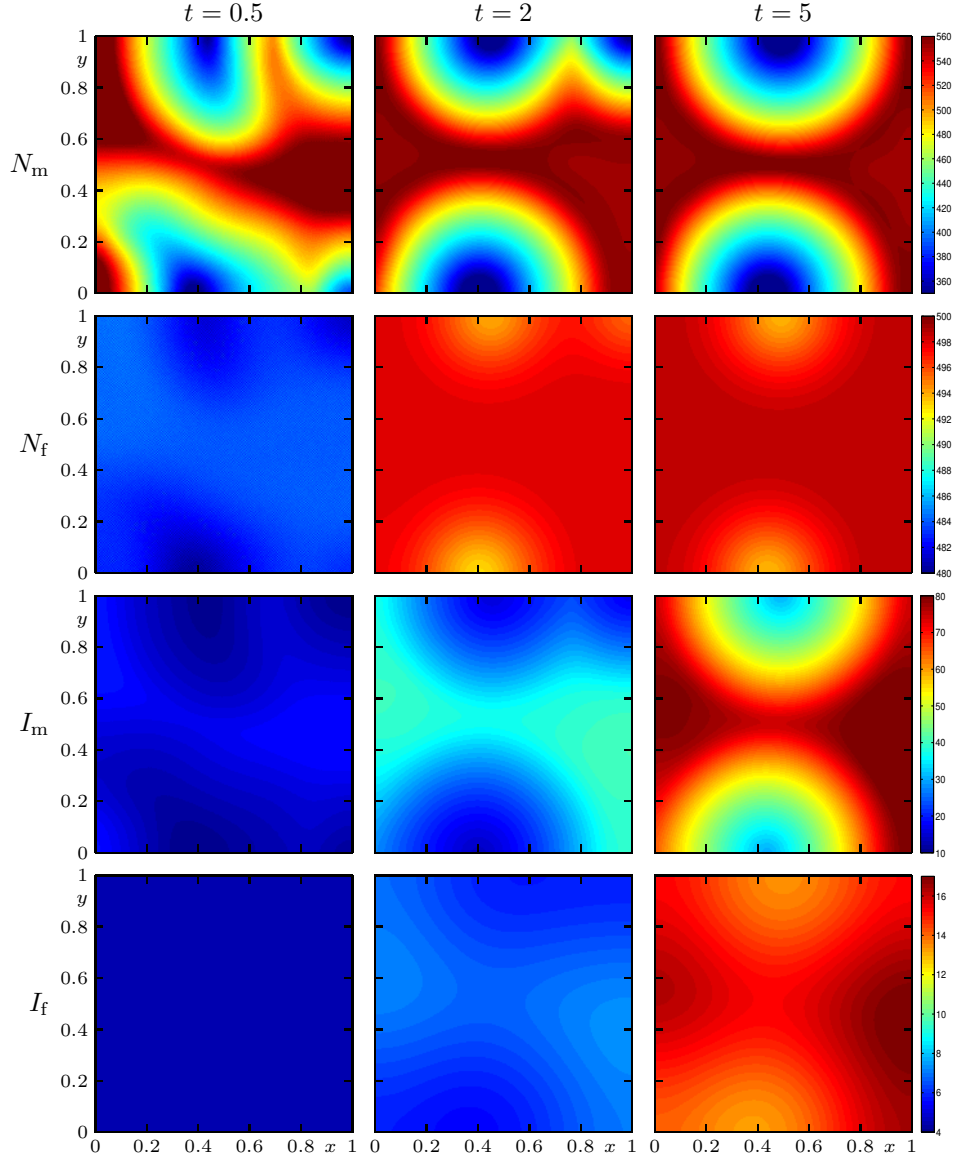


FIGURE 8. Case 6 (Model 3, Scenario 2): numerical solution for N_m , N_f , I_m and I_f at the indicated times.

aggregate in a kind of filamentous structure, including some marked peaks with N_m reaching values close to 3000. On the other hand, we observe the formation of areas of roughly the same shape and size that are nearly void of male individuals. This behavior is similar to that observed by Colombo and Rossi for the predator density in their predator-prey model (cf., e.g., [17, Figs. 3.3–3.5]). In our cases, the densities of the female populations N_f and I_f do not vary much over the computational domain, and do so smoothly. For the same scenario with Model 2 and $K = 1000$, Figure 7 indicates that while for small times we observe the formation of spatial

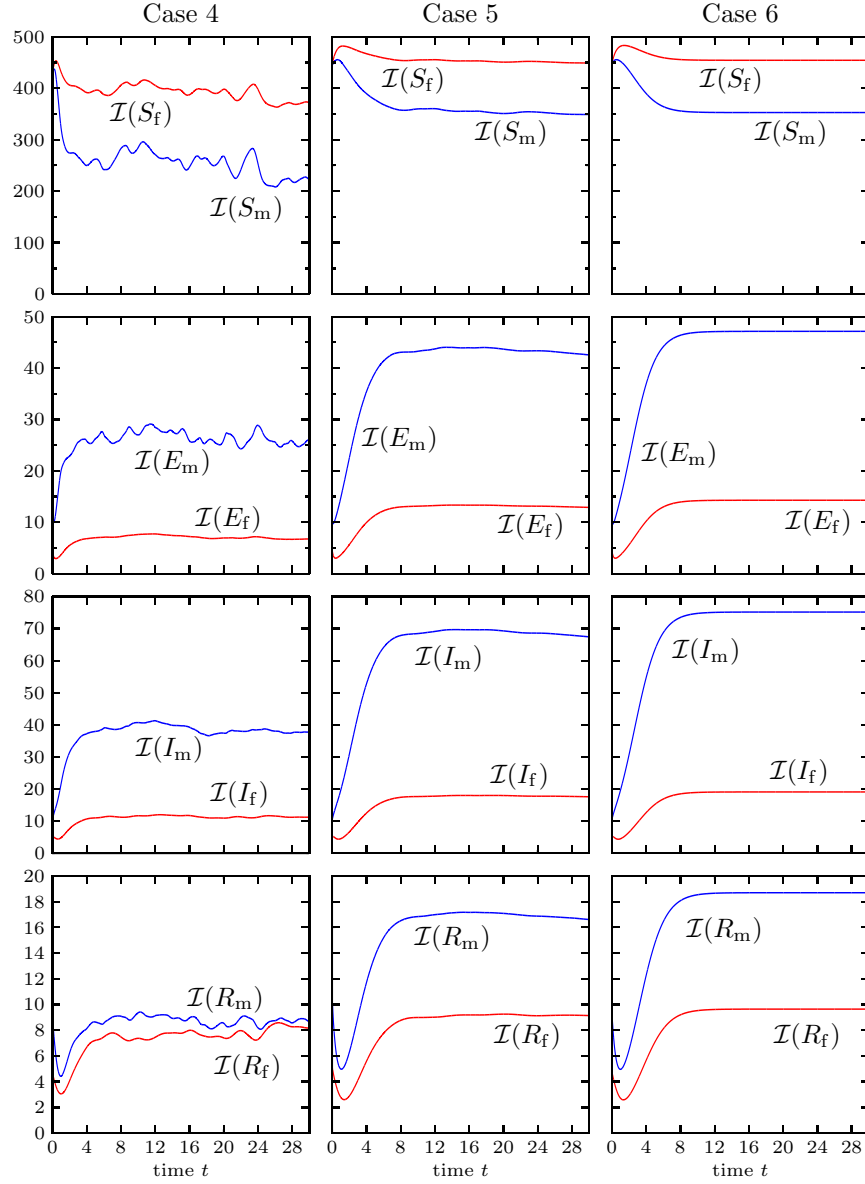


FIGURE 9. Cases 4–6: integral quantities $\mathcal{I}(X)$ defined by (3.3) for each compartment obtained by evaluating numerical solutions.

structures similar those of Figure 6, eventually all variables become nearly constant on the whole domain. Figure 8 for Model 3 illustrates that marked circular spatial structures persist over long times. Similar results (not shown here) were obtained in other numerical experiments for times up to $t = 87$. We also comment that Figure 9 illustrates that Model 2 leads to a nearly stationary behavior of the integral quantities within shorter time than for Scenario 1, and results for Models 2 and 3 are quite similar. The curves observed for the male compartments within Species 1

are, again, oscillatory, which lends further support to the conjecture that this model (at least with the parameters chosen) exhibits spatial-temporal oscillatory behavior.

4. Conclusions. We have shown that a relatively simple gender-structured spatial-temporal model (1.2) of Hantavirus transmission among rodents with a non-local velocity term (1.7), which arises in each of the Models 1, 2 and 3 defined by (1.3), (1.4) and (1.6), respectively, can yield complex spatial-temporal profiles of disease prevalence (Figures 2 to 8). However, in reality, a number of additional factors can affect the transmission dynamics of Hantavirus infections among rodents. Specifically, the transmission of hantavirus has been associated with land use patterns, elevation, vegetation types [7], as well as temperature, humidity, and rainfall [44]. Moreover, rodent habitat and rodent behavior can be influenced by temperature, precipitation and land use [14]. The growth of rodent populations may also be associated with local temperature, as temperature may affect the pregnancy rate, litter size, birth rate and survival rate of rodent populations [42]. Further, rodents tend to inhabit highly covered and less disturbed habitats, which are commonly found in agricultural habitats and pastureland habitats [29, 43] in order to enhance their reproduction and survival capacity [29].

We plan to conduct further research on the qualitative analysis of the proposed models, or suitable simplifications of them, using analogous techniques to those utilized in [17]. The accuracy of the numerical method proposed in this work is worth to be studied in subsequent works, specially to establish that its order of convergence corresponds to its design order. Although in this work we use a second order spatial discretization of the Laplacian and a second order time-stepping, which limit the high order accuracy of the fifth order WENO spatial semidiscretization, we plan to perform comparisons with higher order discretizations of the diffusion operator and time-stepping scheme. Finally, more scenarios (initial configuration, parameter calibration) should be explored with these numerical tools in order to obtain and study further spatio-temporal patterns in the simulations. In this sense, among our proposed models, we consider that Model 1 is the most promising one giving rise to spatio-temporal patterns and is worth to be analyzed as in [16, 28].

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