

Some mathematical problems arising in heterogeneous insular ecological models

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Abstract. In this note we discuss two deterministic mathematical models found in ecological problems caused by the introduction of alien species into a heterogeneous insular environment. In the first model we develop an epidemic model with indirect transmission of the virus via the environment. In the second model we introduce a specific predator-prey model exhibiting finite time extension of species. Both models involve systems of partial differential equations having interesting features.

Algunos problemas matemáticos planteados en modelos ecológicos insulares heterogéneos

Resumen. En esta nota se analizan dos modelos matemáticos deterministas planteados en problemas ecológicos causados por la introducción de nuevas especies en ambientes insulares heterogéneos. En el primero desarrollamos un modelo epidemiológico con transmisión indirecta del virus por medio del ambiente. En el segundo se introduce un modelo específico de depredador-presa que exhibe la extinción en tiempo finito de las especies. Ambos modelos involucran sistemas de ecuaciones en derivadas parciales con interesantes propiedades.

1. Introduction

We are interested in some deterministic mathematical population dynamics models motivated by ecological problems caused by the introduction of alien species into heterogeneous insular environments. It is commonly observed that naive local populations are quite unable to develop efficient anti-predation or anti-competition strategies, yielding extinction of many native species; see Atkinson [1], Courchamp and Sugihara [9], Pontier *et al.* [28] and references therein. Mathematical models are thus required to, first, better understand interactions between local and newly introduced populations, and second, to help develop and design strategies to protect native populations.

In this note we describe two specific examples involving domestic cats, *Felis catus*, purposely or accidentally introduced in various isolated islands and quickly becoming a dominant predator for native species, i.e. birds, mammals and reptiles; see Atkinson [1], Pontier *et al.* [28] and references therein.

The first example is based on the work in Berthier *et al.* [7]. It is an a posteriori mathematical model devised to understand the obvious success of the eradication program developed in 1977 on Marion Island to eliminate a cat population that was becoming a threat for many native bird species. A highly pathogenous

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virus (feline panleucopenia virus) was introduced in the cat population. A first feature of this virus lies in its two propagation modes: horizontal (from infective to susceptible individuals) and indirect (from contaminated environment to susceptible individuals). Within an average 18 days an infected individual either dies or recovers, while the virus can survive up to one year on infected premises. Compared to standard compartmental epidemic mathematical models of the S.E.I.R type, [8] [14] [27], it becomes necessary to introduce a new state variable taking care of the contamination via the environment. A second feature is the impact of the virus, much stronger on young individuals than on adult ones imposing an age structure. This will lead to a coupled age structured system of partial and ordinary differential equations, having spatially discontinuous coefficients in order to take into account heterogeneous spatial and social structures.

The second example is based on the work in Courchamp and Sugihara [9]. This is a theoretical attempt to model specific interactions between native species and introduced alien predator or competitor species, possibly yielding finite time extinction of some species. In [10] [11] and [12] this work is extended to a three species system; as a typical result it is shown that, under some circumstances, eradicating the top predator can be more harmful to native preys than controlling it to such a level that it can efficiently control the intermediate introduced species. The mathematical tool is a singular system of ordinary differential equations, with a simple functional response to predation as compared to standard ones (see [27] and references in [3]); it offers a variety of dynamical behaviors. This model is developed to take into account spatial heterogeneities. This will lead to a three component system of singular reaction-diffusion equations. Numerical experiments will exemplify typical dynamics.

2. An epidemic model with indirect transmission through contaminated environment

This section is a work still in progress, in the continuation of an earlier model developed in Berthier *et al.* [7], to which we refer for more details and bibliographical references.

In 1949, five domestic cats *Felis catus* were introduced on Marion Island, a 290 km² uninhabited island in southern Indian Ocean. The cat population was estimated at 2100 individuals in 1975, 40% of the cats being kittens, killing about half a million burrowing petrels per year. In March 1977 the cat population reached about 3400 individuals when feline panleucopenia virus (FPLV) was introduced: 96 cats were trapped, inoculated with the virus, and then released. The population size declined to an estimated 600 cats in 1982, with an annual decay of 8%; antibodies found in survival individuals suggested that the virus was unable to eradicate the cat population. An important culling effort, using more conventional methods, led to the eradication of cats in 1992. At least one local species was driven to local extinction.

2.1. The motivating unstructured epidemic model

In most standard unstructured compartmental host-microparasites epidemic models the host population is split into subclasses according to the health status of individuals: Susceptibles, Exposed, Infectives and Recovered (or Removed); see [8]. In [7] this approach is followed first, and it is concluded there that such a model cannot explain the impact of the virus from 1977 to 1982: qualitative properties of solutions to the resulting system of ordinary differential equations did not fit the observed data, e.g. the epidemic curve.

FPLV is resistant to harsh physical conditions: it has been observed that the virus excreted by infective cats could survive about a year on infected premises; this is to be compared to the lengths of the exposed stage (four days) and the infective stage (two weeks). Then, introducing indirect transmission from the contaminated environment to susceptible cats gave reasonably good qualitative results.

Prior to derive an epidemic model, we first look at the population dynamics model without parasite. Let N be the host population density; let $b > 0$ be the natural birth rate, m with $0 < m < b$, the natural death rate, and $m + kN$, $k \geq 0$, the density dependent death rate. In a parasite free setting the host population

dynamics is driven by the ordinary differential equation

$$dN/dt = bN - (m + kN)N, \quad N(0) > 0. \quad (1)$$

When $k = 0$ the host population experiences an exponential growth, while when $k > 0$ it follows a logistic dynamics with a carrying capacity $K = (b - m)/k$, this is $N(t) \rightarrow K$ as $t \rightarrow +\infty$.

Next, ignoring the exposed stage, let S , I and R be the respective densities of susceptible, infective and recovered individuals; thus $N = S + I + R$ is the total population density. Let C , $0 \leq C \leq 1$, be the proportion of the environment contaminated by viruses excreted by infectives. To derive a S.I.R.C. epidemic unstructured model one needs to introduce a set of parameters: e is the percentage of infected hosts subsequently recovering from the disease ($0 < e < 1$), $\alpha > 0$ is the reciprocal of the length of the infective stage, $\rho > 0$ is the rate of indirect transmission of the virus so that ρC is the force of infection of the environment on the host population, ϕ is the rate of transmission of the virus from infectives towards the environment so that ϕI is the force of infection of infective cats on the environment, and δ is the decontamination rate of the environment. A last but important point is horizontal transmission from infective to susceptible individuals given by an incidence term $\sigma(S, I, R)$. No vertical transmission (from infected mother to kittens) being observed, this leads to the following model

$$\begin{aligned} dS/dt &= b(S + I + R) - (m + kN)S - \sigma(S, I, R) - \rho CS, & S(0) > 0, \\ dI/dt &= -(m + kN)I - \alpha I + \sigma(S, I, R) + \rho CS, & I(0) > 0, \\ dR/dt &= -(m + kN)R + e\alpha I, & R(0) \geq 0, \\ dC/dt &= \phi I(1 - C) - \delta C, & C(0) \geq 0. \end{aligned} \quad (2)$$

Then, the impact of the parasite on the host dynamics is seen from the equation for the global host density derived upon adding the first three equations in (2), this is

$$dN/dt = bN - (m + kN)N - (1 - e)\alpha I, \quad N(0) > 0. \quad (3)$$

A rather unclearly settled and controversial issue is the incidence term, see [8], [14], [18]; two of the most popular parametric forms are

$$\sigma(S, I, R) = \begin{cases} \sigma_{pm} \frac{SI}{N}, & \sigma_{pm} > 0, & \text{proportionate mixing,} \\ \sigma_{ma} SI, & \sigma_{ma} > 0, & \text{mass action;} \end{cases} \quad (4)$$

Going back to the motivating cat-FPLV problem, in [7] it is chosen an exponential growth for the cat population, i.e. $k = 0$. Then, both incidence forms from (4) were tested against field data, using numerical simulations and stability analysis of steady states. As a conclusion it is found that a mass action incidence gave better results than a proportional mixing one.

2.2. Heterogeneous structured problems

At least two important features are not incorporated in (2): first, spatial and social heterogeneities, and second, an age structure.

Coupled with or related to food abundance variability, spatial heterogeneities locally modify host densities and social structures in host populations; this is specifically true for domestic cat populations: see Fromont *et al.* [18] and references therein. As a consequence contact rates are also affected, and also transmission rates of parasites. In such circumstances, parasites can take advantage of heterogeneities for locally surviving in some specific small parts of a large spatial domain and control a host population, while a host population can escape a parasite through a reverse process.

A last feature is the fate of infective individuals: 20% of infective adults and 80% of infective kittens die, others develop immunity for about six years and have a normal life expectancy. Introducing an age structure is thus required due to the strong effect of FPLV on kittens; this is the main reason of choosing FPLV to eradicate the cat population that was experiencing an exponential growth with a large percentage of kittens.

2.2.1. A spatially structured model

Let Ω be a bounded domain in \mathbb{R}^n , $n \geq 1$, with sufficiently smooth boundary $\partial\Omega$; η is the unit outward normal to Ω on $\partial\Omega$. The spatially and time dependent state variables are $S(x, t) \geq 0$, $I(x, t) \geq 0$ and $R(x, t) \geq 0$ so that $N(x, t) = N = S + I + R$ is the total population density, while $0 \leq C(x, t) \leq 1$ is the local proportion of contaminated environment.

Spatial heterogeneities are modeled upon defining open sub-domains Ω_ℓ of Ω , $\ell = 1 \cdots L$, with $\overline{\Omega_\ell} \subset \Omega$,

$$\Omega_k \cap \Omega_\ell = \emptyset \text{ for } k \neq \ell, \text{ and letting } \Omega_0 = \Omega - \bigcup_{\ell=1}^L \overline{\Omega_\ell}.$$

In each class, population fluxes take the form $-d_p(x)\nabla P + P\mathbf{c}_p(x)$, $P = S, I, R$; herein, for each P , \mathbf{c}_p is a $C^1(\mathbb{R}^n)$ vector field, and d_p is a piecewise discontinuous and bounded diffusion coefficient satisfying

$$\begin{cases} 0 < d_{min} \leq d_p(x) \leq d_{max} < +\infty, \forall x \in \Omega, P = S, I, R; \\ d_p(x) = d_{p,\ell}(x) \text{ for } x \in \Omega_\ell, d_{p,\ell}(\cdot) \in C(\overline{\Omega_\ell}), \ell = 0 \cdots L. \end{cases} \quad (5)$$

Furthermore more assumes standard continuity properties of densities and fluxes across interfaces, namely

$$(H1) \quad \text{continuous densities } S, I, R \text{ across } \partial\Omega_\ell, \ell = 1 \cdots L,$$

$$(H2) \quad \text{balanced fluxes across } \partial\Omega_\ell, \ell = 1 \cdots L$$

$$[(d_p(x)\nabla P(x, t) - P(x, t)\mathbf{c}_p(x)) \cdot \eta_\ell(x)]_{\partial\Omega_\ell} = 0, P = S, I, R, \quad (6)$$

wherein η_ℓ is a normal unit vector to the boundary $\partial\Omega_\ell$ of Ω_ℓ , and $[\cdot]_{\partial\Omega_\ell}$ stands for the saltus across $\partial\Omega_\ell$. Heterogeneities in the incidence term are modeled upon introducing the characteristic function χ of Ω_0 , and setting for some nonnegative and bounded functions σ_{pm} and σ_{ma} on Ω

$$\sigma(x, S, I, R) = \chi(x)\sigma_{ma}(x)SI + (1 - \chi(x))\sigma_{pm}(x)\frac{SI}{N}. \quad (7)$$

Following [18], Ω_0 would represent a favorable area with middle to large host densities, while for each ℓ , $1 \leq \ell \leq L$, Ω_ℓ would represent less favorable locations with small population densities.

Remaining coefficients are nonnegative and bounded functions on Ω .

This yields the following four component system of partial and ordinary differential equations

$$\begin{cases} \partial S/\partial t - \text{div}(d_s(x)\nabla S - S(x, t)\mathbf{c}_s(x)) = \\ \quad b(x)N - (m(x) + k(x)N)S - \sigma(x, S, I, R) - \rho(x)CS, \\ \partial I/\partial t - \text{div}(d_i(x)\nabla I - I(x, t)\mathbf{c}_i(x)) = \\ \quad -(m(x) + k(x)N)I - \alpha I + \sigma(x, S, I, R) + \rho(x)CS, \\ \partial R/\partial t - \text{div}(d_r(x)\nabla R - R(x, t)\mathbf{c}_r(x)) = -(m(x) + k(x)N)R + e(x)\alpha I, \\ \partial C/\partial t = \phi(x)(1 - C)I - \delta(x)C, \end{cases} \quad (8)$$

supplemented by no-flux boundary conditions on the boundary of Ω

$$(d_p(x)\nabla P(x, t) - P(x, t)\mathbf{c}_p(x)) \cdot \eta(x) = 0, x \in \partial\Omega, t > 0, \text{ for } P = S, I, R, \quad (9)$$

corresponding to isolated populations and a set of nonnegative and bounded initial conditions

$$\begin{aligned} P(x, 0) = P_0(x) \geq 0, \text{ for } P = S, I, R, \\ 0 \leq C(x, 0) = C_0(x) \leq 1, \end{aligned} \quad x \in \Omega. \quad (10)$$

Due to the nonnegativity of ϕ and δ , as long as $I(x, t) \geq 0$ it is easily checked that $0 \leq C \leq 1$ is forward invariant by the differential equation for C in (8).

Then, assuming diffusivities to be continuous functions on $\overline{\Omega}$, instead of assuming the second part of (5), uniform estimates can be derived in $L^\infty(\Omega \times (0, T))$, $\forall T > 0$, for the first three components of nonnegative solutions to (8), (9) and (10) upon using duality arguments of Pierre [24] or intermediate sum conditions techniques of Morgan [25]-[26]. As a consequence global existence of suitable nonnegative solutions to (8), (9) and (10) can be proved using standard fixed point methods.

But these $L^\infty(\Omega \times (0, T))$ norms of solutions depend on the moduli of continuity of diffusivities; a new idea is thus required when the weaker assumption from (5) holds. A similar problem is handled in Fitzgibbon *et al.* [16], imposing some positivity conditions on demographic parameters

$$\exists k_{min} > 0, k_{min} \leq k(x) \leq k_{max} < +\infty. \tag{11}$$

Using this condition one can follow the methodology in [16], this is local a priori estimates, regularity results from [22] and cut-off functions, to get a priori estimates and show in [17]

Theorem 1 *Assume that coefficients in (8) and data in (10) are nonnegative and bounded functions. Assume diffusivities satisfy (5), and assume condition (11) hold.*

Then, problem (8), (9) and (10) has a unique suitable nonnegative solution in $L^\infty(\Omega \times (0, \infty))$. \square

Existence results in $L^1(\Omega \times (0, T))$, $\forall T > 0$, can be derived along the lines of Bendahmane *et al.* [5].

Similar population dynamics mathematical problems are found in various host-parasite systems with indirect transmission in heterogeneous environment, e.g. [29].

This is also the case for indirect contamination by chemical pollutions or nuclear wastes.

2.2.2. An age-dependent and spatially structured model

Introducing an age structure can be done, using standard techniques [4], [21] and [30].

As in [15] two age variables are required: chronological age a , with $0 \leq a \leq A_\dagger$, for susceptibles, infectives and recovered, and age of the disease b , with $0 \leq b \leq \tau$, for infectives; A_\dagger is the maximal life expectancy of individuals and τ is the length of the infective stage, i.e. $\alpha = 1/\tau$ from subsection 2.1.

State variables are densities $s(x, t, a)$ for susceptibles with $0 \leq a \leq A_\dagger$, $i(x, t, a, b)$ with $0 \leq b \leq \max(a, \tau)$ for infectives and $r(x, t, a)$ with $\tau \leq a \leq A_\dagger$ for recovered.

Both constraints $0 \leq b \leq \max(a, \tau)$ for infectives and $\tau \leq a \leq A_\dagger$ for recovered are imposed by the lack of vertical transmission of immunisation. Set $\tau(a) = \max(a, \tau)$.

Spatial densities are retrieved upon integrating over age(s)

$$S(x, t) = \int_0^{A_\dagger} s(x, t, a) da, I(x, t) = \int_0^{A_\dagger} \int_0^{\tau(a)} i(x, t, a, b) db da, R(x, t) = \int_\tau^{A_\dagger} r(x, t, a) da, \tag{12}$$

and one still has $N = S + I + R$.

The system of ordinary and partial differential equations governing the dynamics of the age structured host-parasite system needs to be modified. One has for $x \in \Omega, t > 0$ and $0 \leq a \leq A_\dagger$

$$\begin{aligned} \partial s / \partial t + \partial s / \partial a - \operatorname{div}(d_s(x, a) \nabla s - s(x, t, a) \mathbf{c}_s(x, a)) = \\ -\mu(x, a, N) s - \sigma(x, a, s, i, r) - \rho(x, a) C s, \end{aligned} \tag{13}$$

where μ is the age dependent death rate of susceptible and recovered individuals; then, for $x \in \Omega, t > 0$ and $0 \leq a \leq A_\dagger$ and $0 \leq b \leq \tau(a)$

$$\partial i / \partial t + \partial i / \partial a + \partial i / \partial b - \operatorname{div}(d_i(x, a, b) \nabla i - i(x, t, a) \mathbf{c}_i(x, a)) = -\mu_i(x, a, b, N) i, \tag{14}$$

where μ_i is the age specific death rate of infectives ($0 \leq \mu(x, a, N) \leq \mu_i(x, a, b, N)$); last, for $x \in \Omega, t > 0$ and $\tau \leq a \leq A_\dagger$

$$\partial r / \partial t + \partial r / \partial a - \operatorname{div}(d_r(x, a) \nabla r - r(x, t, a) \mathbf{c}_r(x, a)) = -\mu(x, a, N) r + i(x, t, a, \tau). \tag{15}$$

The equation for C remains the same

$$\partial C / \partial t = \phi(x)(1 - C)I - \delta(x)C. \tag{16}$$

No-flux boundary conditions corresponding to an isolated population are imposed on $\partial\Omega$

$$(d_s(x, a)\nabla s(x, t, a) - s(x, t, a)\mathbf{c}_s(x, a)) \cdot \eta(x) = 0, \quad x \in \partial\Omega, \quad t > 0, \quad 0 < a < A_{\dagger}, \tag{17}$$

with similar boundary conditions for i and r .

A set of nonnegative and bounded initial conditions is given at $t = 0$

$$\begin{cases} s(x, 0, a) = s_0(x, a) \geq 0, \quad x \in \Omega, \quad 0 < a < A_{\dagger}, \\ i(x, 0, a, b) = i_0(x, a, b) \geq 0, \quad x \in \Omega, \quad 0 < a < A_{\dagger}, \quad 0 < b < \tau(a), \\ r(x, 0, a) = r_0(x, a) \geq 0, \quad x \in \Omega, \quad \tau < a < A_{\dagger}, \\ 0 \leq C(x, 0) = C_0(x) \leq 1, \end{cases} \tag{18}$$

with $i_0(x, a, b) = 0$ for $0 \leq a \leq b$, corresponding to a lack of vertical transmission of the disease. A set of initial conditions at $a = 0$ for susceptibles, in $0 \leq a \leq b \leq \tau$ for infectives, and on $0 \leq a \leq \tau$ for recovered individuals describes the birth-process and the lack of vertical transmission of the disease

$$\begin{cases} s(x, t, 0) = \int_0^{A_{\dagger}} \beta(x, a) \left(s(x, t, a) + r(x, t, a) + \int_0^{\tau(a)} i(x, t, a, b) db \right) da, \\ i(x, t, a, b) = 0, \quad 0 \leq a \leq b \leq \tau, \\ r(x, t, a) = 0, \quad 0 \leq a \leq \tau; \end{cases} \tag{19}$$

herein, $\beta(x, a) \geq 0$ is the natural birth rate of individuals, assuming the virus has no impact on the fertility of infected individuals.

Last, the recruitment in the infective class, this is infectives having an infection age 0, is given by the susceptible individuals contaminated by either horizontal or indirect transmission

$$i(x, t, a, 0) = \sigma(x, a; s, i, r) + \rho(x, a)Cs, \quad x \in \Omega, \quad t > 0, \quad 0 < a < A_{\dagger}. \tag{20}$$

In order to complete this age-structured model one needs to give some explicit form for the incidence term. Along the lines of [8] and [15], two typical forms for $\sigma(x, a; s, i, r)$ are

$$\int_0^{A_{\dagger}} \int_0^{\tau(a')} \sigma_{pm}(x, t, a, a', b) \frac{i(x, t, a', b)}{s(x, t, a') + \int_0^{\tau(a')} i(x, t, a', b) db + r(x, t, a')} db da' s(x, t, a), \tag{21}$$

and

$$\int_0^{A_{\dagger}} \int_0^{\tau(a)} \sigma_{ma}(x, t, a, a', b) i(x, t, a', b) db da' s(x, t, a). \tag{22}$$

A heuristic analysis along the characteristic lines of $\partial/\partial t + \partial/\partial a$ and $\partial/\partial t + \partial/\partial a + \partial/\partial b$ shows solutions to (13), (14), (15) and (13), satisfying the initial and boundary conditions in (17), (18), (19) and (20) should stay nonnegative with $i(x, t, a, b) = 0$ for $0 \leq a \leq b$.

Existence results can be derived upon combining methods of [15], [23] and [31].

Assuming the virus has an impact on the fertility of infected individuals and still no vertical transmission, the equation for $s(x, t, 0)$ in (19) should be modified into

$$s(x, t, 0) = \int_0^{A_{\dagger}} \left(\beta_s(x, a)s(x, t, a) + \int_0^{\tau(a)} \beta_i(x, a, b)i(x, t, a, b) db + \beta_r(x, a)r(x, t, a) \right) da.$$

3. A predator-prey model with naive preys, introduced preys and alien predators

This section is in the follow up of Courchamp and Sugihara [9] and Courchamp *et al.* [10]-[11]-[12] to which we refer for more details and bibliographical references.

As it is outlined in the Introduction, alien predators introduced in isolated insular environments can cause severe ecological problems, e.g. extinction of native species in the long run or in finite time. The main goal of the model devised in [9] was to analyse the impact of two viruses on the dynamics of a predator in such an insular environment, and to understand how it would help protect native species by controlling the predator. It turns out that this simple predator-prey model is a singular planar system of ordinary differential equation. A mathematical analysis shows it exhibits very interesting dynamics, including finite time extinction of both species.

Built on the same ideas, a three component singular system is considered in [10]-[11]-[12]. Some mathematical analysis is performed to understand the respective ecological pressure put on native species by a top predator (a cat) and either an intermediate predator (a rat and mesopredation effect) or an intermediate competitor (a rabbit and hyperpredation effect).

3.1. The motivating model from Courchamp and Sugihara [9]

This is a two component system of ordinary differential equations. States variables are U the prey density and W the predator density, i.e. birds and cats in the original paper.

Prior to introduction of alien predators it is assumed that the prey population has reached a stable equilibrium, the carrying capacity K of the environment. This means U is a solution to a differential equation similar to (1) with $k > 0$ and $r_u = b_u - m_u > 0$, so that $K = r_u/k$.

Next, define μ as the annual individual intake of prey per individual predator, so that U/μ becomes the carrying capacity for the predator population. Let $r_w = b_w - m_w > 0$ be the natural growth rate of predators. The simple model of [9] does not include realistic predator functional response, e.g. a Holling type II functional response to predation (see Murray [27] and references in [3]), in order not to complicate it, and reads

$$\begin{cases} dU/dt = r_u \left(1 - \frac{U}{K}\right) U - \mu W, & U(0) > 0, \\ dW/dt = r_w \left(1 - \mu \frac{W}{U}\right) W, & W(0) > 0. \end{cases} \quad (23)$$

From a mathematical point of view (23) is a singular system of ordinary differential equations at $U = 0$; it is not totally obvious that nonnegativity of solutions is preserved, as well as global existence granted.

In order to settle these two points it is convenient to introduce a new state variable, $Q = W/U$ the proportion of predators per prey. In the state variables (Q, U) one gets a nonsingular system of ordinary differential equations preserving nonnegativity

$$\begin{cases} dU/dt = r_u \left[1 - \frac{U}{K} - \mu Q\right] U, & U(0) > 0, \\ dQ/dt = \left[r_w - r_u + r_u \frac{U}{K} - \mu(r_w - 1)Q\right] Q, & Q(0) > 0, \end{cases} \quad (24)$$

with complicated dynamics depending on r_w and r_u ; see [19]. When $r_w > 1$ it is rather straightforward to check one has global existence with a global attractor in the (U, W) state variables, e.g. $(0, 0)$ for $r_u \leq 1$ and (U^*, W^*) with positive components for $r_u > 1$. When $0 < r_w < 1$ various local behavior can be exhibited in the (U, W) state variables: finite time extinction for $0 < r_u < r_w < 1$, coexisting local attractors $(0, 0)$ and (U^*, V^*) with positive components for $r_u + r_w > 2$, a local attractors $(0, 0)$ and a Hopf bifurcation along $r_u + r_w = 2$, and finite or infinite time extinction elsewhere.

3.2. A spatially structured model with introduced preys

Many islands located in southern Indian Ocean exhibit heterogeneous landscape offering various types of shelters to native and introduced species. This is the case for Kerguelen Islands where it is observed that

native birds are primarily found along the ocean side, introduced rabbits or rats are found in the center of islands, with cats settled everywhere. Intermediate distribution with coexistence of three populations may or may not be found depending on local environmental conditions.

One natural way of trying to model these patterns is to consider a three components singular reaction-diffusion system with spatially heterogeneous coefficients based on [9] and models in [10], [11] and [12]. A preliminary analysis is performed in [19] for the bird-rabbit-cat system of [11] with spatially variable coefficients along the lines of subsection 2.2. It formally reads

$$\begin{cases} \partial U/\partial t - (\operatorname{div}(d_u(x)\nabla U - U\mathbf{c}_u(x))) = r_u \left(1 - \frac{U}{K_u}\right) U - \lambda UV - \frac{\omega U}{\omega U + V} \mu_u W, \\ \partial V/\partial t - (\operatorname{div}(d_v(x)\nabla V - V\mathbf{c}_v(x))) = r_v \left(1 - \frac{V}{K_v}\right) V - \frac{V}{\omega U + V} \mu_v W, \\ \partial W/\partial t - \operatorname{div}(d_w(x)\nabla W - W\mathbf{c}_w(x)) = r_w \left(1 - \mu_u \mu_v \frac{W}{\mu_u V + \mu_v U}\right) W, \end{cases} \quad (25)$$

supplemented by no-flux boundary conditions on the boundary of Ω

$$(d_p(x)\nabla P(x,t) - P(x,t)\mathbf{c}_p(x)) \cdot \eta(x) = 0, \quad x \in \partial\Omega, \quad t > 0, \quad \text{for } P = U, V, W, \quad (26)$$

corresponding to isolated populations and a set of nonnegative and bounded initial conditions

$$P(x,0) = P_0(x) \geq 0, \quad \text{for } P = U, V, W, \quad x \in \Omega. \quad (27)$$

Herein, λ is a nonnegative parameter modeling a decrease of the bird population induced by rabbits, e.g. hyperpredation in [12]. Last, cats are known to prey on different species according to their availability. For $\omega = 1$, fractions $\frac{\omega U}{\omega U + V}$ and $\frac{V}{\omega U + V}$ represent the respective proportions of birds and rabbits in the prey population; native populations being less adapted to predation, $\omega > 1$ represents a preference effect of cats for birds.

An exhaustive mathematical analysis of this singular three component reaction-diffusion system is not straightforward; for the underlying system of ordinary differential equations some results are found in [11] and [19]. Such a mathematical analysis, concerning global existence vs finite time extinction, is the aim of some undergoing work for the two component system in the (U, W) state variables deduced from (25) (26) and (27) upon setting $V = 0$, or built directly from (23). Much help is to be expected from Díaz and Hernández [13] or Hernández et al. [20], and references therein, where related problems are handled for scalar equations whose solutions have a dead core.

A further mathematical problem is a control problem. It follows from results in [11] and [28] that eradicating the cat population in finite time can have undesirable side effects.

Some general global existence results in heterogeneous environments and stabilization results for more standard predator-prey systems are found in [2], [3] and [6].

3.3. Some numerical experiments

Numerical experiments are performed in [19] on (25) (26) and (27), for constant and small diffusivities and ignoring advection terms. As long as we were more interested in middle to long term behavior we chose positive initial data not to handle short range problems caused on transient solutions by nonnegative data.

The goal was to analyze whether large time spatial coexistence of various dynamics predicted by the underlying system of differential equation (see [11]) can be simultaneously observed through numerical simulations. More specifically we are interested in mimicking the extinction of either U or V on some spatial sub-domains and persistence of the three species elsewhere, a pattern observed on Kerguelen islands, [28].

Some care is required to handle singular terms. One of the most efficient way is to modify singular terms, this is proportions of prey U and prey V in the equations for U and V in (25). A simple choice is to introduce a small parameter $\nu > 0$; then, substitute $\frac{\omega U}{\omega U + V + \omega \nu}$ to $\frac{\omega U}{\omega U + V}$ in the equations for U , and $\frac{V + \nu}{\omega U + V}$ to $\frac{V}{\omega U + V}$ in the equations for V .

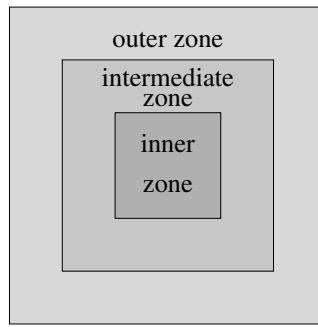


Figure 1. Spatial domain.

Then, choosing a set of positive initial data, a suitable splitting method proved efficient, and gave reasonably good results.

In Figure 1, Ω is the unit square in \mathbb{R}^2 , split into three radial pieces, an inner square, an outer and an intermediate zones. The set of growth rates used in numerical simulations for each population in each sub-domain is given in Table 1; for each set of parameter values solutions to the underlying system of ordinary differential equations exhibit different dynamics, as depicted above: coexistence of the three species in the intermediate zone and extinction of one prey species in each of the other two zones.

	r_u	r_v	r_w	λ	ω	μ_u	μ_v	K_u	K_v
inner zone	0.05	3	0.95	0	1.5	180	180	1000	800
intermediate zone	2	3	0.95	0	1.5	180	180	1000	800
outer zone	2	0.05	0.95	0	1.5	180	180	1000	800

Table 1: Set of parameter values.

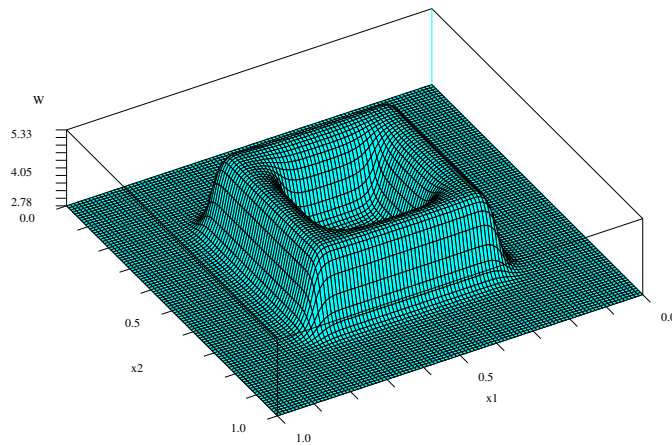


Figure 2. Alien predator population.

In Figure 2 to Figure 4 numerical results for solutions to the heterogeneous system (25), (26) and (27) with positive initial data, small and constant diffusivities and no advection are displayed.

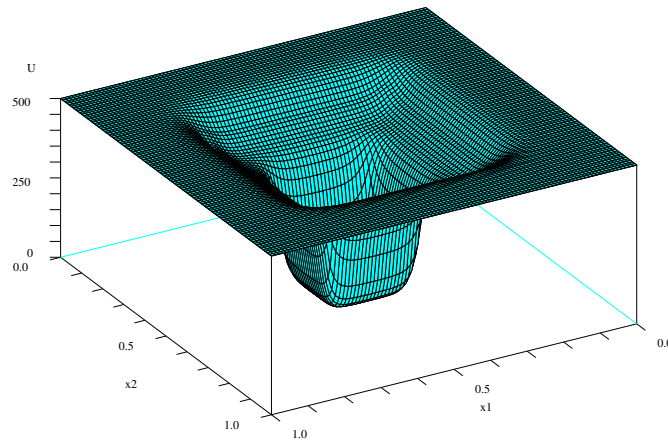


Figure 3. Native prey population.

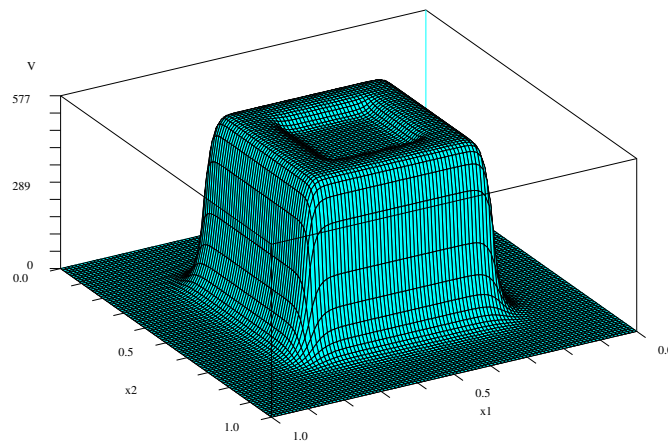


Figure 4. Introduced prey population.

One may observe extinction of the introduced intermediate prey in the outer zone, extinction of the native prey in the inner zone, and coexistence of the three species in the intermediate zone.

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