Mathematical model and numerical simulation of the population dynamics of *capybaras*: an epizootic model with dispersal, migration and periodically varying contagion

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Abstract. In this paper we present a justification for a single-species model, with dispersal and migration characteristics, as well as a compartmental division of the population in order to obtain an epizootic model, with a periodically varying contagion rate. The numerical method used is described and numerical results are presented and commented.

Key-words: Population dispersal; population dynamics; epizootic modelling; Finite Elements; variable contagion rate.

1. Introduction

In the years from 1999 through to 2001 the authors were part of a group which, under the leadership of Rossi, C., from the University of Siena, studied several different aspects of the *Iberá* region, in northeastern Argentina, as part of the project "The sustainable management of wetland resources in Mercosul" (Rossi and others, 1999). Part of these studies involved the population dynamics of certain charismatic species with regards to ecotourism – and its positive influence insofar as strategies of natural conservation as well as the survival of local human populations are concerned. This problem appeared in a more general picture: that of a sustainable community.

Previous authors have presented the case for efficient modelling and simulation of population dispersal problems with the use of systems of partial differential equations (see Gurney and Nisbet, 1975; Cosner, 1996; Murray, 1989; Pregnolatto, 2002). Cosner and others have argued in favour of more research with this kind of modelling effort. In agreement with Skellam's suggestion, as well as that of Kareiva's population dispersal characterization, both of which chose the route of linear short-term PDE (in the sense of not being significantly affected by the population dynamics), we intend, here, in a similar attitude, to propose the use of a system with which we can undertake the study of a cyclic epizootic problem that arose in a general study of *capybara*[3] (*Hydrocoerus hydrochaeris*) population dynamics and dispersal.

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[3] "Capybara" in the local *Tupy-Guarany* language, "Grass-eater"

Capybaras are the greatest rodents that exist, and may weigh well over 100 pounds in adult individuals, which may reach 1.30m in length. They live in groups that vary from 20 to 30 individuals; they are gregarious and always live near water. Two or three times a year, they mate, and litters are from 4 to 6 offspring. Their greatest activities are at the beginning and at the end of the day – they have nocturnal and diurnal habits. They are prey to american pumas and occasionally, to the local *"yacaré"*, south-american crocodiles, besides, of course, humans. They co-exist peacefully with livestock.

Although we do recognize the need for the study certain species from the point of view of eco-systems, an approach which seems to exclude the modelling of single populations, and in spite of the fact that *capybaras* are not quite at end of the trophic chain in many environments, nevertheless, the option here is for a study of the *derengadera* disease in local populations, with these animals being considered here in the single population picture.

This disease severely affects this species in the *Iberá* region, and local park rangers refer to it as having the effect of literally exterminating the *capybara* population every seven years or so. The adopted choice of modelling this single species implies that some simplification is necessary and, indeed, what can justify this attitude is the possibility of executing numerical simulations with which initial approximations can be studied and experience obtained with which to grow from in the sense of adopting improved models, numerical methods and computer algorithms.

2. Description of modelling choices

The model we have opted for in this case is one that considers both a population dispersal model, in the above-mentioned sense, as well as compartmental models for the epizootical considerations. Previous modelling efforts in this direction, that is to say, combining spatial distribution, population dynamics and diseases have been presented by Thieme (1977), Shigesada (1980), Capasso and Madalena (1981), Webb (1982), Keeling and Grenfell (1997), Grasman (1998), as well as Murray (1989) – this latter including the study of travelling diseases.

The innovative aspect of the model we present is in combining of a non-linear population dynamics (for which we have adopted a Verhulst-type of evolutionary dynamics, although other choices could have been made), descriptive of the reproductive characteristics of the studied species included in a classical compartmental epidemiological model (using the traditional term, although the case is that of an epizootical situation).

The proposed mathematical tool therefore combines population dynamics modelling with that of population dispersal for the traditional compartments S, I, M, functions of the space variables $(x,y) \in \Omega \subset R^2$ and of a temporal variable, $t \in (0, T] \subset R^1$. These represent the three compartments into which the entire population is divided: $S=S(x,y,t)$, the susceptibles, $I=I(x,y,t)$, the infected and $M=M(x,y,t)$ the removed, or deceased animals. The non-linear system of differential equations we present is:

$$\frac{\partial S}{\partial t} - \nabla \bullet (k_S \nabla S) + V_S \bullet \nabla S + \sigma_S.S = \lambda S(1 - \frac{(S+I)}{K}) - \alpha.S.I,$$

$$\frac{\partial I}{\partial t} - \nabla \bullet (k_I \nabla I) + V_I \bullet \nabla I + \sigma_I.I = \alpha.S.I - \beta I, and \tag{1}$$

$$\frac{\partial M}{\partial t} = \beta I, \text{ for } (x, y) \in \Omega \text{ and } t \in (0, T].$$

In this system, the parameters are:
1. k_S and k_I respectivelly stand for dispersion coefficients for healthy and afflicted *capybaras*;
2. V_S and V_I represent (possible) migration tendencies, in the form of vector fields;
3. σ_S and σ_I stand for environmental hostilities for both susceptible and infected individuals – for which different values are expected, since infected animals disperse considerably less than susceptibel ones;
4. λ is the intrinsic reproduction rate for susceptible animals, and only for these, since infected individuals do not reproduce;
5. α is the rate of infection, inducing the change of compartment, from the susceptible to the infected state; and, finally
6. β is the mortality rate for infected *capybaras*.

Non-linearities arise in the first two equations of system (1) due to the chosen dynamics as well as the infection process. In the first equation, on the right side, the first term combines the Verhulst-like dynamics including susceptible and infected animals in the environmental limitation but not in the reproduction – since infected animals do not reproduce.

3. The chosen model

System (1) does not, in itself, represent a new model, but a suggestion from BASSANEZI (2000), changing the characteristic of the infection rate, introduces a relevant modification:

$$\frac{\partial S}{\partial t} - \nabla \bullet (k_S \nabla S) + V_S \bullet \nabla S + \sigma_S.S = \lambda S(1 - \frac{(S+I)}{K}) - \alpha(t).S.I$$

$$\frac{\partial I}{\partial t} - \nabla \bullet (k_I \nabla I) + V_I \bullet \nabla I + \sigma_I.I = \alpha(t).S.I - \beta I \qquad (2)$$

$$\frac{\partial M}{\partial t} = \beta I, \text{ for } (x, y) \in \Omega \text{ and } t \in (0, T], \text{ and for}$$

$$\alpha(t) = \alpha_0 + \beta_0.sin\frac{6t+\gamma}{\pi}, \text{ t considered in months.}$$

In this second model, a variation of the first one, in fact, three new parameters are introduced:
1. α_o is the mean reproduction rate for the considered insect species;
2. β_0 is the scope of the variation in the reproduction rate; and
3. γ is used in order to adjust the variation to the chosen time scale.

The purpose of this change is to introduce a periodical behaviour of the population of insects, which act as the disease vectors. These can be of several types, but the most common in the region are the *mutucas* (Diptera Tabanideae) the population of which has a dynamic aspect which can be approached in he form of a sinus, with maximum population in the wet season, that is to say in summer, and a minimum in population in the driest season, which is the local winter.

System (1) is a non-linear system of partial differential equations, with constant coefficients in the epidemiological[4] part of the model. System (2) introduces a modification in one of these constants: from a fixed parameter α into a function of time: an approach to the periodical effect of cyclic variations in population levels of the disease-inducing insect and, consequently, in the infection rate.

Both systems (1) and (2) are sufficiently complex as to challenge mathematicians and applied mathematicians alike: both analytic solutions as well as numerical ones present considerable difficulties, some of them quite serious.

4. Initial and boundary conditions

The considered domain, as is quite common in initial studies, is a rectangle. Now this may, sometimes, discourage ecologists (who work with maps and regions) in their contacts with applied mathematicians, but there are two arguments in favour of the use of these "special" domains in initial stages of modelling and simulation:

- first, there have been many simulations upon rectangular domains using systems of diffusive-advective systems and this may signify that there are "expected" behaviours for numerical solutions, a pattern against which the obtained results can be matched and, if necessary, discarded;

- a second reason, which mathematicians do not, in general, state, is that the chosen domain may very often be considered as homeomorphic to the chosen, original, domain, and a transformation could be used to transform the results (when presented in the form of level curves, for example) from a well-behaved rectangle to the original, natural, map-like domain.

The initial condition chosen for the numerical simulations was to consider a constant distribution of the susceptible population, no dead individuals, and a small quantity of infected individuals at a point along the region's boundary.

The adopted boundary conditions intend to simulate situations which effectively occur: along parts of the boundary there are no individuals; on other parts, natural boundaries exist so that there is no movement or passage of individuals leaving or entering the domain and, finally, there are parts of the boundary along which there is such a passage, and it is proportional to the local population. In other words, considering the boundary of the domain $\Omega \subset \mathbb{R}^2$ as $\partial\Omega = \Gamma_0 \cup \Gamma_1 \cup \Gamma_2$ with disjoints subsets Γ_i.

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[4] The term epidemiological is not correct since it refers to diseases in human, the appropriate term should be epizootical. Nonetheless, the term is adopted here in the mathematical sense, which identifies a system with Kermack and McKendrick characteristics (see Murray, J.D.)

The stated boundary conditions can now be expressed as:

$$S\big|_{\Gamma_0} = 0,\ I\big|_{\Gamma_0} = 0,\ M\big|_{\Gamma_0} = 0,$$

$$\frac{\partial S}{\partial \eta}\bigg|_{\Gamma_1} = 0,\ \frac{\partial I}{\partial \eta}\bigg|_{\Gamma_1} = 0,\ \frac{\partial M}{\partial \eta}\bigg|_{\Gamma_1} = 0, \qquad (3)$$

$$\frac{\partial S}{\partial \eta}\bigg|_{\Gamma_2} = \mu S,\ \frac{\partial I}{\partial \eta}\bigg|_{\Gamma_2} = \mu I,\ \frac{\partial M}{\partial \eta}\bigg|_{\Gamma_2} = 0.$$

where the parameter μ represents a permeability constant standing for the proportion of local population, which crosses the mentioned part of the boundary. The deceased individuals are evidently not considered in this last situation.

Analytic solutions, as mentioned previously are not considered in this work, although the existence and uniqueness will be part of a different paper since the purpose of this work is to present the model and some of the numerical simulations.

5. Discretization and approximation

In order to be able to use theoretical results which can guarantee not only existence of solutions, but convenient orders of convergence in numerical results, and considering the possibility of using the resulting algorithms in irregular map-like domains, the option will be for the Finite Element Method in discretizing space variables.

This choice implies in a Galerkin Method variable separation, so that a Finite Difference scheme can be adopted in the time variable. In fact, the natural choice here indicates an Implicit Crank-Nicholson scheme, and the combination of these choices permits second-order approximations in space and in time. This strategy implies that: (i) the variational formulation will used instead of the classical one, given by the above defined systems; and (ii) S(x,y,t), I(x,y,t) and M(x,y,t) will be approximated using:

$$S(x,y,t) \cong \sum_j S_j(t).\phi_j(x,y),$$

$$I(x,y,t) \cong \sum_j I_j(t).\phi_j(x,y), \text{ and} \qquad (4)$$

$$M(x,y,t) \cong \sum_j M_j(t).\phi_j(x,y).$$

In this triple substitution functions S_j, I_j, M_j are functions only of the time variable t, whereas functions ϕ_j are of the space variables (x,y). These are the test functions of the Finite Element Method,which means that the domain Ω is also approximated by $\Omega_h{}^5$, the discretized domain. Substitution of these approximations in (2) transforms the PDE system into a system of ODE's, given by:

$$\sum_j \frac{dS_j(t)}{dt}.(\phi_j\,|v) + \sum_j S_j(t).(k_S\nabla\phi_j\,||\,\nabla v) +$$

$$+ \sum_j S_j(t).(V_S\cdot\nabla\phi_j\,|v) + (\sigma_S - \lambda)\sum_j S_j(t).(\phi_j\,|v) =$$

$$- \sum_j S_j(t).\left[\frac{\lambda}{K}.\sum_k S_k(t).(\phi_j\phi_k\,|v) + \alpha\sum_k I_k(t).(\phi_j\phi_k\,|v)\right],$$

$$\sum_j \frac{dI_j}{dt}(t).(\phi_j\,|\,v) + \sum_j I_j(t).(k_I\nabla\phi_j\,||\,\nabla v) + \sum_j I_j(t).(V_I\cdot\nabla\phi_j\,|v) +$$

(5)

$$+ (\sigma_I + \beta)\sum_j I_j(t).(\phi_j\,|v) = \alpha.\sum_j I_j(t).\left[\sum_k S_k(t).(\phi_j\phi_k\,|v)\right], and$$

$$\sum_j \frac{dM_j}{dt}(t).(\phi_j\,|\,v) = \beta.\sum_j I_j(t).(\phi_j\,|\,v),$$

for $\forall v \in V$, a conveniently defined space.

This non-linear system also presents analytic difficulties of such an order as to justify approximating it by a numerical scheme. The choice, as mentioned previously, is for the Crank-Nicolson method, and the reason for adopting this implicit scheme is its second order approximation in time, besides its being unconditionally stable. This means that instead of calculating the values of functions $S_j(t)$, $I_j(t)$ and $M_j(t)$ on the successive time-steps t_n, that is, $S_j(t_n)$, $I_j(t_n)$ and $M_j(t_n)$, the scheme will calculate the values $S_j^{(n)}$, $I_j^{(n)}$ and $M_j^{(n)}$. This leads to the substitution of the differential terms in (5) – for all three sets of functions S_j , I_j and M_j – by the corresponding Crank-Nicolson operators. This will lead to another non-linear system, although no longer a system of differential equation. Classical methods can be used for approximating solutions. In this case, we resort to the successive linearization approach, in fact a predictor-corrector second-order scheme (see Douglas and Dupont, 1970).

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[5] This means that although Ω_h and Ω may, eventually be different, as $h\to0$, then $\Omega\to\Omega_h$, in a certain sense, with h representing in some way the 'size' of the discretization.

6. Visualization of numerical results

The above-mentioned algorithm was programmed in a Matlab® environment and results were treated using this software's resources for visualization possibilities. Initial and boundary conditions are those mentioned in the beginning of paragraph 4, and population dispersal parameters are considered to be constant in the domain, since this is practically what actually happens on dry land in the region.

Each figure presents six different aspects of one of the simulations: the first three figures show three-dimensional graphs of surfaces with the final spatial distribution of, respectively, susceptible, infected and deceased individuals over the generic domain; the next three figures represent a certain spatial point of the domain along time, giving the local population level for, likewise, susceptible, infected and deceased populations. In spite of the obviously artificial rectangular form of the domain used in the programme, the purpose is that of obtaining information on the behaviour of both the model and the algorithmic approach, and matching these to what local information can be obtained. Analysis of the first three shows that the population of infected animals subsists where susceptibles were previously: susceptibles become infected and these, in turn, become deceased, and the third graph shows this sequence. The population level of susceptibles is very low, but still there is a variation, from which a population come-back could, under certain circumstances, be obtained. The last three graphs emphasize these same conclusions for population levels at a certain point as time goes by: in fact, the third graph shows that, while infected populations survive, the population of dead animals is still increasing.
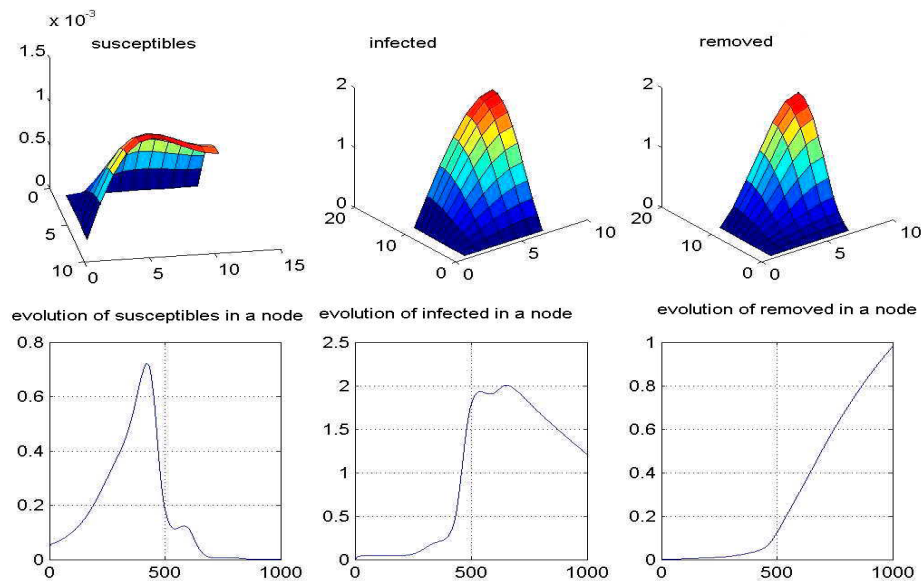

Figure 1: Simulation for 1 000 steps in the time.

7. Comments and conclusions

The results are promising in the sense that it would very important to run the programme using a geographically appropriate model, and with conveniently obtained parameters. Observation of the obtained figures exhibits both the expected complementary coupled behaviour of the numerical solutions as well as situations affected by the introduced periodic variation in contagion. Aspects of classical behaviours for Susceptible-Infected were as to be expected, as well as the growth of deceased animals along the general time-period. This model, however, was not designed as to include the population comeback from the extremely low values for susceptible individuals. For this it would be necessary to include both the dynamics for the infecting insect as well as the interaction between the *capybaras* and these insects.

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