J. Math. Anal. Appl. 399 (2013) 352–368

Contents lists available at SciVerse ScienceDirect

Journal of Mathematical Analysis and Applications

journal homepage: www.elsevier.com/locate/jmaa

# Persistence and extinction in spatial models with a carrying capacity driven diffusion and harvesting☆,☆☆

L. Korobenko, Md. Kamrujjaman, E. Braverman *

*Department of Mathematics and Statistics, University of Calgary, 2500 University Drive N.W., Calgary, AB T2N 1N4, Canada*

ARTICLE INFO

*Article history:*
Received 13 September 2012
Available online 11 October 2012
Submitted by Yuan Lou

*Keywords:*
Diffusion
Harvesting
Positive periodic solution
Global attractivity
Rate of convergence
Logistic law
Gilpin–Ayala growth
Gompertz function
Maximal yield

ABSTRACT

For the reaction–diffusion equation

$$\frac{\partial u(t,x)}{\partial t} = D\Delta\left(\frac{u(t,x)}{K(t,x)}\right) + r(t,x)u(t,x)g\left(K(t,x),u(t,x)\right) - E(t,x)u(t,x)$$

with the general type of growth, diffusion stipulated by the carrying capacity $K$ and harvesting, existence, positivity, persistence, extinction and stability of solutions are investigated. In numerical simulations, the results are compared to the model with a regular diffusion.



## 1. Introduction

A natural way to introduce spatial movements in the models of population dynamics is to add a diffusion term into the right-hand side of the equation, which in many cases leads to the uniform ideal free distribution (see, for example, [1,2]). For models with unequally distributed resources (nonconstant carrying capacity of the environment), this may lead to the possibility of massive migration from the places with high per capita available resources to less fertile areas, which is a questionable strategy. Moreover, the fitness of the population decreases as the diffusion coefficient increases [3]. This leads to an unreasonable conclusion that the ability to disperse quicker leads to evolutionary disadvantages. There have been several other approaches adopted for describing movements in models of fire or disease spread, chemotaxis models and some other models—see the recent papers [4–6] and references therein; there have also been attempts to correct the ideal free distribution by introducing an advection term in the direction of higher per capita available resources, so that the density of the population tends to the carrying capacity for large times if the advection to diffusion ratio is very high [7,8]. In [9] Cantrell et al. considered a system of two competing species which use different diffusion strategies: one of the strategies discussed in the paper is the ideal free dispersal strategy when the density of the species matches the carrying capacity of the resources. The authors also established some important results on persistence, extinction, and coexistence of the competing populations with similar growth laws and dispersal strategies.

As mentioned in [10], a null model for habitat patch selection in spatially heterogeneous environments is the ideal free distribution, which assumes that individuals have complete knowledge about the environment and can disperse freely; see

☆ The research of L. Korobenko was partially supported by a PIMS IGTC scholarship.

☆☆ E. Braverman was partially supported by an NSERC research grant.

* Corresponding author.
*E-mail addresses:* lkoroben@ucalgary.ca (L. Korobenko), mkamrujj@ucalgary.ca (M. Kamrujjaman), maelena@math.ucalgary.ca (E. Braverman).

0022-247X/$ – see front matter © 2012 Elsevier Inc. All rights reserved.
doi:10.1016/j.jmaa.2012.09.057

also [11]. Under the equilibrium conditions, this model predicts that local population growth rates are zero in all occupied patches, sink patches are unoccupied, and the fraction of the population selecting a patch is proportional to the patch's carrying capacity.

It is also believed (see, for example, [12]) that the number of grazing animals is related to the primary productivity (carrying capacity) of the environment. When considering invasive species, for example, *Solanum carolinense* from North America in Europe [13], it is assumed that without control (harvesting), it will spread over the whole continent, according to the available resources (mainly, climate-related issues were considered).

In [14], it was demonstrated that for non-homogeneous environments any type of purely diffusive behavior, characterized by symmetric migration rates, produces an unbalanced population distribution, i.e. some locations receive more individuals than can be supported by the environmental carrying capacity, while others receive fewer. Using an evolutionarily stable strategy approach, the authors show that an asymmetric migration mechanism, induced by the heterogeneous carrying capacity of the environment, will be selected.

Whether the grazing animals population [12], or invasive weeds [13] or other species, or insects [15], or North American prairie ducks [16] are chosen, the observations indicated that the dispersal is asymmetric, directed to the areas of more available per capita resources. The environment properties can include productivity of food supply for herbivores, climate parameters, and human hosts for *Aedes aegypti* [15].

Along the lines of the above mentioned observations, we consider the carrying capacity driven diffusion where species diffuse not to less congested areas but in the direction of higher per capita available resources. This model was first introduced in [17]; stability properties of the equation with the logistic type of growth were first studied in [18]. One important observation that should be made here is about the way we introduce a diffusion term in the equation. Usually, in the case of random dispersal of species the diffusion term takes the form $\nabla \cdot d\nabla u$, where $d$ is the diffusion coefficient, and $u$ is the density of the species. In this case the dimension of $d$ is $m^2/s$. However, in the case of carrying capacity driven diffusion presented here, the diffusion term has the form $D\Delta(u/K)$ where $K$ is the carrying capacity of the environment and has the same dimensionality as $u$. Therefore, this new diffusion coefficient has dimension $m^{2-n}/s$ where $n$ is the dimension of space (usually, 1, 2 or 3), and should not be interpreted in the same way as $d$. When comparing the above mentioned models with two different types of diffusion, to equate the diffusion coefficients one should put $d = D/K$.

Along with non-homogeneous growth and spatial dispersal, harvesting can be involved as a part of the dynamics. This may correspond to predation, for example, in analyzing plant production in the presence of herbivores [12], human harvesting, or weed [13] or pest control.

In this paper, we obtain the following main results.

1. For a general model with time and space variable growth law, harvesting and carrying capacity, the existence and uniqueness theorem, as well as persistence and extinction conditions, is presented.
2. For time-independent growth law and carrying capacity, if the intrinsic growth exceeds the harvesting effort, there is a positive stationary solution, which under certain conditions attracts all positive solutions. For variable periodic parameters, there is a similar result for either a positive periodic solution or the zero equilibrium.
3. Numerical simulations confirm the theoretical results, while comparing the two models (with two different diffusion types) and partially exploring the feasible situation where harvesting exceeds the intrinsic growth rate in some parts of the domain and is smaller in the other parts.

Compared to the regular type of diffusion model, the model with the carrying capacity driven diffusion has the following advantages:

1. For time-independent carrying capacity, the ideal free distribution coincides with the carrying capacity, independently of the diffusion coefficient.
2. In the case of the logistic growth, there is an advantage compared to the regular (random) diffusion independently of the diffusion coefficient [19].
3. If the carrying capacity is time independent, an optimal continuous harvesting strategy can be developed [17] which to some extent leads to maximal yield over all possible harvesting and diffusion scenarios; see also [20] and Section 7 of the present paper.

The paper is organized as follows. After the problem is stated and several particular cases are considered in Section 2, existence, permanence and extinction of solutions are investigated in Section 3. Section 4 considers the case where the growth law, the carrying capacity and the harvesting effort are time independent. Under certain conditions, all positive solutions converge either to zero or to a positive stationary solution; in the absence of harvesting, this stationary solution coincides with the carrying capacity. In Section 5, the case of periodic parameters is studied, in particular the existence of a positive periodic solution and its attractivity. Section 6 involves numerical simulations. Finally, Section 7 contains some discussion and presents open problems.

## 2. Statement of the problem

We consider the following model:

$$\frac{\partial u(t,x)}{\partial t} = D\Delta\left(\frac{u(t,x)}{K(t,x)}\right) + f(t,x,u(t,x)) - E(t,x)u(t,x), \quad (t,x) \in Q_T \tag{2.1}$$