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A Mathematical Model for the Propagation of an Animal Species on a Plain

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Abstract

A mathematical model for the dynamics of an animal species propagating on a plain is constructed. Travelling wave solutions are then sought for two cases, the case with constant diffusion coefficient and that with density-dependent diffusion coefficient. The results show the existence of travelling wave solutions in both cases. The existence of travelling wave solutions for the two-dimensional model is important as it captures more realistically the physical interactions of species in a habitat. The minimum wave speeds as well as the basins of attraction were determined. The results also indicate the occurrence of a saddle-node bifurcation in the case with density-dependent diffusion coefficient. The basins of attraction in both cases are functions of the wave speed and is still a subject for further investigation.

Keywords: Travelling wave, density-dependent diffusion, basin of attraction, equilibrium point.

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1 Introduction

Animal species such as human beings, cattle, goats, sheep and others propagate on land. They move about freely and interact with one another. In the case of a single species, say cattle, we are interested in examining the dynamics of propagation on a plain. A model of this nature was developed by Fisher in 1937 for the propagation of an advantageous gene in humans. In the current research, we add a natural mortality rate as it is natural for animal species to die. An important aspect of this work is the method of analysis of the model equation. Researchers such as Murray(2002), Kot (2001), Akubo (2001) and Debnath (2005) have analysed similar equations by seeking travelling wave solutions. In particular, Murray (2002) obtained the exact travelling wave solution of the Fisher equation. In the current research, a two-dimensional reaction-diffusion model will be constructed and analysed using the travelling wave solution procedure. The two-dimensional model captures the physical situation more realistically, yet not much studies have been done on it. Two cases of the model will be considered, the cases of constant and density-dependent diffusion coefficients. Mansour (2008) analysed a nonlinear partial differential equation with density-dependent diffusion coefficient using the travelling wave approach and obtained approximate and exact travelling wave solutions using Taylor's series expansion method. We shall use asymptotic approximation to obtain approximate travelling wave solutions similar to that of Debnath (2005). This approach enables us obtain the approximate equations of the heteroclinic orbits, which will be the confirmation of the existence of travelling wave solutions, apart from the conditions outlined by Billingham and King (2000) for the existence of such solutions. Numerical solutions to similar problems have been obtained by Mansour (2007), Mansour (2008) and Ndam *et al* (2012). Fassoni *et al* (2014) reported that parameter values in a competition model determine the shape and size of the basins of attraction of the equilibria and could also influence the outcome of the competition.The basins of attraction of the models will be determined and the biological implications outlined. The remaining parts of this paper are organised as follows: Section 2 deals with the mathematical formulation of the model, the travelling wave solution and analysis of the model with constant diffusion coefficient will be carried out in section 3, while the travelling wave solution of the density-dependent diffusion coefficient model will be the subject of section 4. Section 5 will be dedicated to Results and Discussions. Finally, conclusions will be the subject of section 6.

2 Mathematical formulation

The model equation governing the propagation of an animal species on land is given by the Fisher-KPP equation in two dimensions

$$u_t = D\left(u_{xx} + u_{yy}\right) + ru\left(1 - \frac{u}{K}\right) - au \tag{1}$$

where $D > 0$ is the diffusion coefficient, which is the rate at which the species move on land, $r > 0$ is the linear growth rate, $K > 0$ is the carrying capacity of the environment, and $a > 0$ is the natural death rate, since the species can die of natural causes or harvesting, hence $a \ll 1$. The species undergo a logistic growth subject to the carrying capacity of the environment as captured by the term $ru\left(1 - \frac{u}{K}\right)$. The term $D\left(u_{xx} + u_{yy}\right)$ on the other hand, captures the random mass movement of the animal species on the field.

We now scale the equation to get rid of the many parameters and to make the equation dimensionless for ease of analysis. Using the non-dimensional variables x^*, y^*, t^*, a^* and u^* defined by

$$x = \sqrt{\frac{D}{r}}x^*, y = \sqrt{\frac{D}{r}}y^*, t = \frac{t^*}{r}, a = ra^*, u = Ku^*,$$

where $\sqrt{\frac{D}{r}}$ represents the length scale, we obtain after dropping asterisks, the equation

$$u_t = u_{xx} + u_{yy} + u(1 - u) - au \tag{2}$$

Diffusion in this case refers to the number of animals that pass through a unit area per unit time measured in m^2/s. The diffusion coefficient can be constant if the species are assumed to move approximately uniformly on land. Moreover, diffusion coefficient can be density-dependent, which reflects the effects of population size on the dispersal of the species. Details of this can be found in Okubo (2001). In reality, the movement of animal species can be hindered by their number, hence density-dependent diffusion models capture more realistically the patterns of movement of species than the simple constant diffusion models. The model equation (1) with density-dependent diffusion coefficient $D(u)$, becomes

$$u_t = [D(u)u_x]_x + [D(u)u_y]_y + ru\left(1 - \frac{u}{K}\right) - au \tag{3}$$

Using the same scalling variables above, the scaled model equation becomes

$$u_t = [d(u)u_x]_x + [d(u)u_y]_y + u\,(1-u) - au \tag{4}$$

where $d(u) = \frac{D(u)}{D}$ and D is some typical coefficient of diffusion.

3 Travelling wave solution and stability analysis

The Fisher-type model equation with constant and density-dependent diffusion coefficients admit a travelling wave solution of the form

$$u(x, y, t) = u(z) \tag{5}$$

where $z = \alpha x + \beta y - ct$, c is the constant wave speed, while α and β are constants. Using the variable z in (2) leads to the second order nonlinear ordinary differential equation

$$u'' + \delta u' + bu(1 - a - u) = 0 \tag{6}$$

where $\delta = \frac{c}{\kappa^2}$, $b = \frac{1}{\kappa^2}$, $\kappa^2 = \alpha^2 + \beta^2$ and $u' = \frac{du}{dz}$. Reducing (6) to a first order system of ordinary differential equations becomes

$$u' = v, v' = -\delta v - bu(1 - a - u) \tag{7}$$

The system (7) has the equilibrium points $(u, v) = (0, 0)$ and $(u, v) = (1 - a, 0)$ which represent the steady states. The Jacobian matrix associated with this system is given by

$$J(u, v) = \begin{pmatrix} 0 & 1 \\ -b(1 - a - 2u) & -\delta \end{pmatrix}$$

Thus, the Jacobian matrix at the equilibrium point $(0, 0)$ is given by

$$A(0, 0) = \begin{pmatrix} 0 & 1 \\ -b(1 - a) & -\delta \end{pmatrix}$$

which has the characteristics equation

$$\lambda^2 + \lambda\delta + b(1 - a) = 0$$

with the eigenvalues

$$\lambda_1 = \frac{-\delta + \sqrt{\delta^2 - 4b(1 - a)}}{2}, \lambda_2 = \frac{-\delta - \sqrt{\delta^2 - 4b(1 - a)}}{2}.$$

Hence, the origin is a stable node for $\delta^2 - 4b(1 - a) \geq 0$, that is, $c^2 \geq 4\kappa^2(1 - a)$. Hence the minimum wave speed c_m is then given by $c_m = 2\kappa\sqrt{(1 - a)}$.

On the other hand, the Jacobian matrix corresponding to the equilibrium point $(1 - a, 0)$ is given by

$$A(1 - a, 0) = \begin{pmatrix} 0 & 1 \\ b(1 - a) & -\delta \end{pmatrix}$$

with the characteristic equation

$$\lambda^2 + \delta\lambda - b(1 - a) = 0.$$

The eigenvalues are obtained as

$$\lambda_1 = \frac{-\delta + \sqrt{\delta^2 + 4b(1 - a)}}{2}, \lambda_2 = \frac{-\delta - \sqrt{\delta^2 + 4b(1 - a)}}{2}.$$

Thus, $(1-a,0)$ is a saddle point. Hence the existence of a physically meaningful travelling wave originating from the point $(1-a,0)$ and terminating at the origin has been established.

We now obtain the equations of the stable and unstable manifolds as follows: Let ξ_1 and ξ_2 be the eigenvectors corresponding to the eigenvalues λ_1 and λ_2 respectively. Thus

$$\Rightarrow \xi_1 = \begin{pmatrix} -1 \\ \delta - \sqrt{\delta^2 + 4b(1-a)} \end{pmatrix}, \xi_2 = \begin{pmatrix} -1 \\ \delta + \sqrt{\delta^2 + 4b(1-a)} \end{pmatrix}.$$

The general eigensolution is then given by

$$W = (u(z), v(z))^T = \begin{pmatrix} -C_1 e^{\lambda_1 z} - C_2 e^{\lambda_2 z} \\ C_1\left(\delta - \sqrt{\delta^2 + 4b(1-a)}\right) e^{\lambda_1 z} + C_2 \left(\delta + \sqrt{\delta^2 + 4b(1-a)}\right) e^{\lambda_2 z} \end{pmatrix} \tag{8}$$

where C_1 and C_2 are arbitrary constants. Hence

$$\frac{dv}{du} = -\frac{\lambda_1 C_1\left(\delta - \sqrt{\delta^2 + 4b(1-a)}\right) e^{\lambda_1 z} + \lambda_2 C_2 \left(\delta + \sqrt{\delta^2 + 4b(1-a)}\right) e^{\lambda_2 z}}{\lambda_1 C_1 e^{\lambda_1 z} + \lambda_2 C_2 e^{\lambda_2 z}}.$$

Thus, for $C_1 = 0$,

$$\frac{dv}{du} = -\left(\delta + \sqrt{\delta^2 + 4b(1-a)}\right) \Longrightarrow v(u) = -\left(\delta + \sqrt{\delta^2 + 4b(1-a)}\right) u + A,$$

where A is a constant to be determined. Since $v(0) = 0$, we obtain the equation of the stable manifold v_{sm} as

$$v_{sm} = \frac{(1-a-u)}{\kappa^2}\left[c + \sqrt{c^2 + 4\kappa^2(1-a)}\right] \tag{9}$$

Similarly, the equation of the unstable manifold v_{um} is given by

$$v_{um} = \frac{(1-a-u)}{\kappa^2}\left[c - \sqrt{c^2 + 4\kappa^2(1-a)}\right] \tag{10}$$

The basin of attraction is given by the region R_1 in the uv-plane defined by

$$R_1 = \left\{(u,v) : u = 0, v = 0, v = \frac{(1-a-u)}{\kappa^2}\left[c - \sqrt{c^2 + 4\kappa^2(1-a)}\right]\right\}.$$

The estimated area of this trapping region is

$$A_1 = \frac{(1-a)^2}{2\kappa^2}\left[\sqrt{c^2+4\kappa^2(1-a)}-c\right]$$

From the system (7), the heteroclinic orbit from $(0,0)$ to $(1-a,0)$ satisfies the equation

$$\frac{dv}{du} = \frac{-\delta v - bu(1-a-u)}{v} \tag{11}$$

Now, we define $v = \frac{1}{c}y$, hence we obtain the equation

$$\epsilon y y' + \frac{y + u(1-a-u)}{\kappa^2} = 0 \tag{12}$$

where $y' = \frac{dy}{du}$ and $\epsilon = \frac{1}{c^2} << 1$ for $c \geq 3$. Now, expanding y as a power series in ϵ as

$$y(u,\epsilon) = y_0(u) + \epsilon y_1(u) + \epsilon^2 y_2(u) + \cdots$$

and using this in (12) leads to the sequence of equations

$$O(1) : \frac{y_0 + u(1-a-u)}{\kappa^2} = 0 \tag{13}$$

$$O(\epsilon) : y_0 y_0' + \frac{y_1}{\kappa^2} = 0 \tag{14}$$

$$O(\epsilon^2) : y_0 y_1' + y_1 y_0' + \frac{y_2}{\kappa^2} = 0 \tag{15}$$

Solving (13) in (14) for y_0 and y_1, yield

$$y_0 = -u(1-a-u), y_1 = \kappa^2 u(1-a-u)(2u+a-1).$$

Thus one obtains the approximate equation of the heteroclinic orbit

$$v = -\epsilon^{\frac{1}{2}} u(1-a-u) + \epsilon^{\frac{3}{2}} \kappa^2 u(1-a-u)(2u+a-1) + \cdots \tag{16}$$

To obtain the travelling wave solution in the physical plane, we use equation (6) with the change of variable $s = \frac{z}{c}$. Hence we obtain the equation

$$\epsilon u'' + bu' + bu(1-a-u) = 0 \tag{17}$$

where $u' = \frac{du}{ds}$. Equation (17) happens to be a regular perturbation problem, since the resulting first order equation when $\epsilon \approx 0$ satisfies the boundary conditions

$$\lim_{z\to-\infty} u = 1-a$$

and

$$\lim_{z\to\infty} u = 0.$$

Thus we expand u in terms of powers of ϵ as

$$u(s,\epsilon) = u_0(s) + \epsilon u_1(s) + \epsilon^2 u_2(s) + \cdots \tag{18}$$

Now, using (18) in (17) produces the following sequence of equations

$$O(1) : u_0' + u_0(1 - a - u_0) = 0 \tag{19}$$
$$O(\epsilon) : u_0'' + bu' + bu_1(1 - a - 2u_0) = 0 \tag{20}$$
$$O(\epsilon^2) : u_1'' + bu_2' - bu_1^2 + bu_2(1 - a - 2u_0) = 0 \tag{21}$$

Equation (19) has the general solution

$$u_0(s) = \frac{C(1-a)}{C + e^{(1-a)s}}.$$

Taking $u_0(0) = 1$, noting that u is invariant under the transformation $s = \frac{z}{c}$, we obtain the solution

$$u_0(s) = \frac{1-a}{1 - ae^{(1-a)s}}.$$

The solution of (20) subject to the condition $u_1(0) = 0$ is obtained as

$$u_1(s) = \frac{(1-a)e^{(1-a)s}}{b\left(1 - ae^{(1-a)s}\right)^2} \ln\left[\frac{e^{(1-a)s}}{\left(1 - ae^{(1-a)s}\right)^2}\right].$$

Hence the approximate expression for the travelling wave solution in the physical plane in terms of z, and thus the space and time variables becomes

$$u(z) = \frac{1-a}{1 - ae^{(1-a)\frac{z}{c}}} + \epsilon\frac{(1-a)e^{(1-a)\frac{z}{c}}}{b\left(1 - ae^{(1-a)\frac{z}{c}}\right)^2} \ln\left[\frac{e^{(1-a)\frac{z}{c}}}{\left(1 - ae^{(1-a)\frac{z}{c}}\right)^2}\right] + \cdots \tag{22}$$

which is valid for $-\infty < z < \frac{c}{1-a}\ln\left(\frac{1}{a}\right)$. The plot for (22) is depicted on figure 4(a).

4 Model with density-dependent diffusion coefficient

Assuming a travelling wave variable of the form $z = \alpha x + \beta y - ct$, and substituting in (4), we obtain the second order ODE

$$\kappa^2 \left[d(u)u'' + u'^2 d_u(u)\right] + cu' + u(1-a-u) = 0 \tag{23}$$

For simplicity, we define $d(u) = u^n$ and using the transformations $u' = v, u^n \frac{d}{dz} = \frac{d}{d\tau}$, we obtain from (23), the system of first order equations

$$u' = u^n v \tag{24}$$

$$v' = -\frac{1}{\kappa^2}\left[cv + u(1-a-u)\right] - nu^{n-1}v^2 \tag{25}$$

where $u' = \frac{du}{d\tau}$. The system of equations (24) and (25) has the equilibrium points $(0,0)$ and $(1-a,0)$ for $n \neq 1$. However, for $n = 1$, the system has the equilibrium points $(0,0), (1-a,0)$ and $(0, -\frac{c}{\kappa^2})$. Standard phase-plane analysis shows that $(0,0)$ is a nonlinear stable node, while the points $(1-a,0)$ and $(0,-\frac{c}{\kappa^2})$ are saddle points. It is possible to have a heteroclinic orbit linking $(0,0)$ and $(1-a,0)$, thus establishing the existence of a travelling wave solution for the model equation with density-dependent diffusion coefficient. Another possible heteroclinic connection is that along the $v-$axis from $(0,-\frac{c}{\kappa^2})$ to $(0,0)$ as can be seen from figure 2. The equation of the unstable manifold for the case with $n = 1$ is given by

$$v_{um}^d = \frac{c}{\kappa^2}\left(\frac{u}{1-a} - 1\right) \tag{26}$$

Using (26), the basin of attraction is the region R_2 defined by

$$R_2 = \left\{(u,v) : u = 0, v = 0, v = \frac{c}{\kappa^2}\left(\frac{u}{1-a} - 1\right)\right\}.$$

This region has the area $A_2 = \frac{c(1-a)}{2\kappa^2}$ squared unit.

The equation of the heteroclinic orbit in the moving frame is given by

$$\frac{dv}{du} = -\frac{cv + u(1-a-u)}{\kappa^2 u^n v} - \frac{nv}{u} \tag{27}$$

Substituting $v = \frac{1}{c}y$ in (27) yields the equation

$$\epsilon y y' + \frac{y + u(1-a-u)}{\kappa^2 u^n} + \frac{\epsilon n y^2}{u} = 0 \tag{28}$$

Now, expanding y in terms of powers of ϵ as

$$y = y_0(u) + \epsilon y_1(u) + \epsilon^2 y_2(u) + \cdots$$

and using it in (28) leads to the following sequence of equations.

$$O(1) : \frac{y_0 + u(1-a-u)}{\kappa^2 u^n} = 0 \tag{29}$$

$$O(\epsilon) : y_0 y_0' + \frac{y_1}{\kappa^2 u^n} + \frac{n y_0^2}{u} = 0 \tag{30}$$

$$O(\epsilon^2) : \frac{y_2}{\kappa^2 u^n} + y_0 y_1' + y_1 y_0' + \frac{2n y_0 y_1}{u} = 0$$

From (29),

$$y_0(u) = -u(1-a-u).$$

Thus, from (30), one obtains

$$y_1(u) = -\kappa^2 u^n \left[y_0 y_0' + \frac{n y_0^2}{u} \right] = \kappa^2 u^{n+1} (1-a-u) \left[(n+2)u - (n+1)(1-a) \right].$$

The equation of the heteroclinic orbit from the point $(1-a, 0)$ to the point $(0, 0)$ is then given by

$$v(u, \epsilon) = -\epsilon^{\frac{1}{2}} u(1-a-u) + \epsilon^{\frac{3}{2}} \kappa^2 u^{n+1} (1-a-u) \left[(n+2)u - (n+1)(1-a) \right] + \cdots \tag{31}$$

When $n = 0$, the heteroclinic orbit (31) reduces to (16), the heteroclinic orbit for the constant diffusion model. The travelling wave solution in the the physical plane can be determined from (20) using the transformation $s = \frac{z}{c}$, with $d(u) = u^n$, resulting into the equation

$$\epsilon \kappa^2 \left[u^n u'' + n u^{n-1} u'^2 \right] + u' + u(1-a-u) = 0 \tag{32}$$

In a similar vein, expanding u in terms of powers of ϵ and substituting in (32), for the case with $n = 1$ produces the sequence of equations

$$O(1) : u_0' + u_0(1-a-u) = 0 \tag{33}$$

$$O(\epsilon) : u_1' + \kappa^2 \left[u_0 u_0'' + u_0'^2 \right] + u_1(1-a-2u_0) = 0 \tag{34}$$

The leading order solution (33), subject to the condition $u_0(0) = 1$, as earlier used becomes

$$u_0(s) = \frac{1-a}{1-ae^{(1-a)s}}$$

while the solution of equation (34) produces

$$u_1(s) = \frac{\kappa^2 a(1-a)e^{(1-a)s}}{B(a,s)} \left\{ \ln\left[\frac{e^{(1-a)s}}{1-a}B(a,s)\right] + \frac{3}{B(a,s)} - \frac{3}{a(1-a)} \right\},$$

where $B(a,s) = 1 - ae^{(1-a)s}$. Hence we have the approximate travelling wave solution

$$u(z) = \frac{1-a}{B(a,z)} + \epsilon\frac{\kappa^2 a(1-a)e^{(1-a)\frac{z}{c}}}{B(a,z)} \left\{ \ln\left[\frac{e^{(1-a)\frac{z}{c}}}{1-a}B(a,z)\right] + \frac{3}{B(a,z)} - \frac{3}{a(1-a)} \right\} + \cdots$$

where $B(a,z) = 1 - ae^{(1-a)\frac{z}{c}}, -\infty < z < \frac{c}{1-a}\ln\left(\frac{1}{a}\right)$. The result is plotted in figure 4(b).

5 Results and Discussions

In this work, we have considered two Mathematical models for the dispersal of an animal species on land. One method of analysing such equations is the travelling wave procedure, which has been used in this case. The two models have been shown to admit travelling wave solutions through the use of phase plane analysis. The density-dependent diffusion model was found to undergo a saddle-node bifurcation for $n = 1$, when the diffusion coefficient takes the simple form $d(u) = u^n$. The additional equilibrium point $(0, -\frac{c}{\kappa^2})$ is a saddle, with the vertical axis of the $uv-$plane serving as the unstable manifold. Trajectories from the neighbourhood of $(0, -\frac{c}{\kappa^2})$ either terminate there or enter $(0, 0)$. Similarly, trajectories from the neighbourhood of $(1 - a, 0)$ can only terminate at $(0, 0)$. Hence we can have a heteroclinic connection form $(1 - a, 0)$ to $(0, 0)$. Another possible connection is that from $(0, -\frac{c}{\kappa^2})$ to $(0, 0)$, along the $v-$axis which forms part of the boundary of the basin of attraction for $(0, 0)$, as can be seen in figure 2. The heteroclinic orbits on the moving frame are shown in figures 3 and 4 for $a = 0.01$ and $a = 0.3$ respectively. The orbit corresponding to the density-dependent model for $n = 1$ is slightly longer than that of the model with constant diffusion coefficient as depicted on figures 3 and 4. The difference in the sizes of the orbits is due to the additional equilibrium point created as a result of the bifurcation. The change in the value of the parameter a has no significant effects on the phase-portraits. Putting $n = 0$ into (31), we recover (16), the expression for the heteroclinic orbit for the constant diffusion model Figures 5(a) and (b) are analogues of the connections shown in figure 3 in the physical frame in two-dimensions, generated using the same parameter values. The areas of the basins of attraction for the two models were also computed for $a = 0.01, k = \sqrt{2}$ and $c = 2k\sqrt{(1-a)}$ and the basin of attraction corresponding to the density-dependent diffusion model ($A_2 = 0.697$ sq. unit) for $n = 1$ is clearly greater than that with constant diffusion coefficient ($A_1 = 0.286$ sq. unit).

6 Conclusions

Mathematical models for the dispersal of an animal species in a terrestrial habitat are constructed and analysed. Travelling wave solutions were sought in both cases, and the results show the existence of such solutions in each case. Furthermore, approximate equations of the heteroclinic orbits for the travelling wave were computed. More importantly, the basins of attraction for the equilibrium points were determined and their areas computed. The result indicate that the trapping region is directly proportional to the wave speed in the case with density-dependent coefficient of diffusion for the particular case with $n = 1$, while the case with constant diffusion is also a function of the wave speed. A saddle-node bifurcation occurs in the density-dependent diffusion coefficient model for $n = 1$ as can be seen in figure 2 when compared with figure 1. Figures 1 and 2 also show the phase-portraits for the two models, while figures 3, 4 and 5 show the heteroclinic connections in the moving coordinates and on the physical plane respectively.

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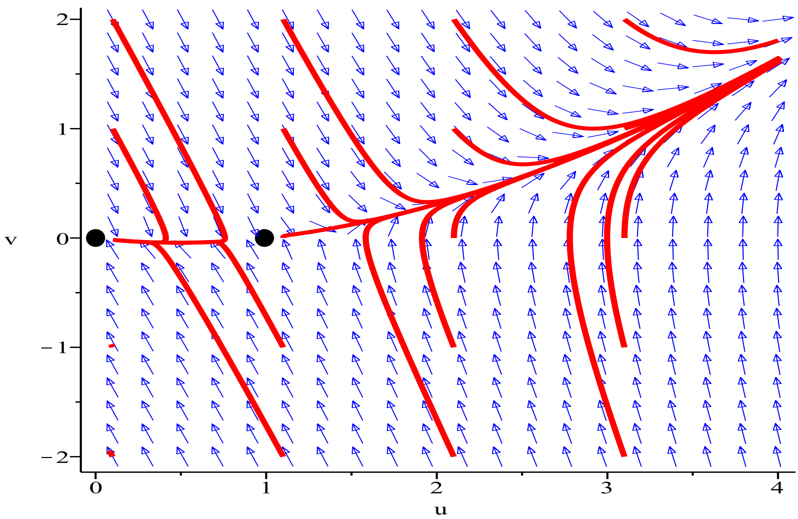


Figure 1: Phase-portrait and trajectories for model with constant diffusion for $a = 0.01, k = \sqrt{2}$ and $c = 2k\sqrt{(1-a)}$

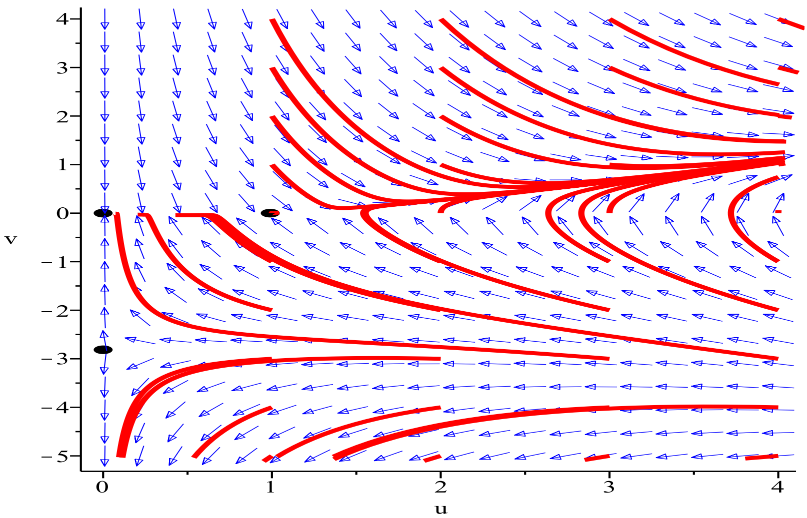


Figure 2: Phase-portrait and trajectories for model with density-dependent diffusion for $a = 0.01, k = \sqrt{2}$ and $c = 2k\sqrt{(1-a)}$

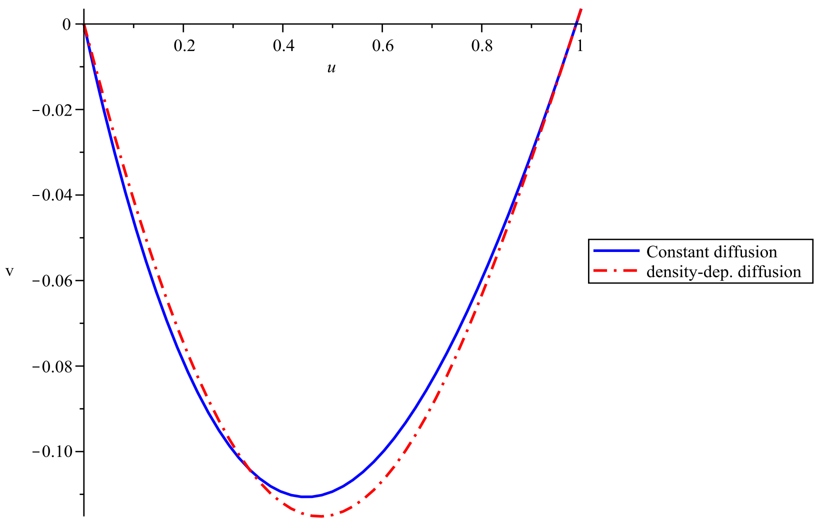


Figure 3: Heteroclinic orbits for the constant and density-dependent diffusion models for $a = 0.01, k = \sqrt{2}$ and $c = 2k\sqrt{(1-a)}$

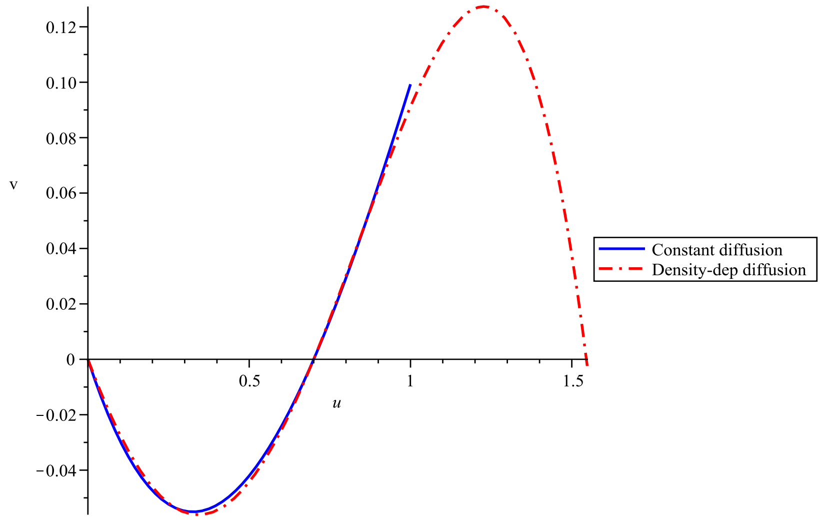
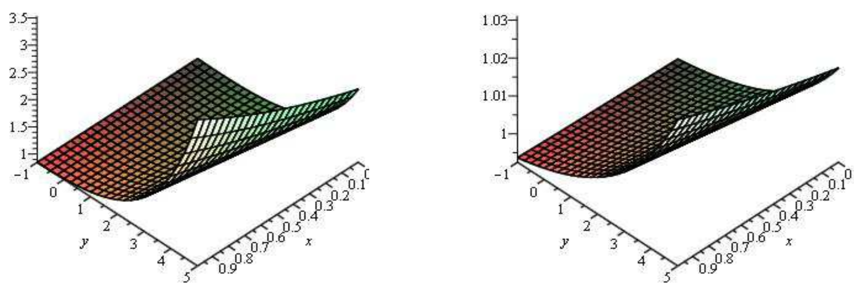


Figure 4: Heteroclinic orbits for the constant and density-dependent diffusion models for $a = 0.3, k = \sqrt{2}$ and $c = 2k\sqrt{(1-a)}$



(a) (b)

Figure 5: 3D heteroclinic orbits for (a) constant diffusion and (b) density-dependent diffusion models for $a = 0.01, k = \sqrt{2}$ and $c = 2k\sqrt{(1-a)}$