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Multi-dynamics of travelling bands and pattern formation in a predator-prey model with cubic growth

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Abstract

We analyse a predator-prey model with cubic growth in which animal movement are incorporated. We focus on the behaviour of the bands of animals to understand the global dynamic of the system. Travelling waves analyses are used to describe the time evolution of the system and to examine the interplay between the bands. We also highlight the influence of individuals behaviours on the collective behaviour of the bands. More importantly, we show the multi-dynamics that diffusion can cause, and we illustrate the patterns formed in the model as a result of a new phenomenon called transport-driven instability. This study shows how sustainable ecosystems could manipulate their movement characteristics to remain stable and viable.

Keywords: travelling waves; pattern formation; predator-prey model; transport equation; cubic growth

1 Introduction

The development of mathematical modelling has proved important in understanding and predicting natural phenomena. In population dynamics, mathematical modelling is used to study the time evolution of population sizes. The first model for population dynamics was proposed by Malthus [1], and its formulation is considered a first principle of population dynamics, known as the Malthusian growth model [2]. The model was formulated on the assumption that a population grows at a constant rate. This resulted generally in unrealistic exponential growth with the explosion of a population over time. To improve the Malthusian growth model, Verhulst [3] incorporated a logistic term. He assumed that growth at an early stage is approximately exponential, then slows with saturation, and stops at maturity. His model is known as the logistic growth model, and has been widely used in ecological modelling to study the different dynamics observed in ecological systems [4–11]. The logistic growth model also has limitations, for it does not consider under or over crowding effects which are important factors. It has been shown that overcrowding effects can affect the psychological responses and health of the system and hence its dynamics [12, 13]. Gilpin (see [14]) proposed a model with a cubic growth function of the form $f(x) = ax - bx^2 + cx^3$ (where the parameters a, b and c are positive) to represent the overcrowding effect in a prey population. Others forms of $f(x)$ have been proposed [15–17]. The cases of systems with oscillatory growth and environment dependent growths

have also been explored [18, 19]. We will use the form of $f(x)$ proposed by Huang *et al.* [20, 21] to study the dynamics in a predator-prey system. Their model is given by

$$
\begin{aligned}
\frac{dx}{dt} &= xf(x) - g(x,y) = x\big(b_1 + b_2x - b_3x^2\big) - b_4xy, \\
\frac{dy}{dt} &= \alpha_1 g(x,y) - yi(y) = \alpha xy - y(\beta y + c),
\end{aligned}
\tag{1}
$$

where x and y are, respectively, the density of prey and predator, the coefficients b_3, b_4, c, α, β are positive, b_1 is non-negative, and the sign of b_2 is undetermined. The function f stands for the per capita growth rate of the prey in the absence of predators, g is the prey death rate due to predation, i is the per capita death rate of predators, and α_1 is the predator efficiency rate.

One of the advantages of the model (1) is that it considers the (weak) allee effect in the prey population (the per capital growth rate of the prey can be written in the form $f(x) = \gamma(x - K_0)(K - x)$, where $\gamma > 0$, $K > 0$ and $K_0 < 0$) [22–25]. The allee effect is a phenomenon in which the fitness of a population decreases as the population size declines [26–28]. The allee effect can be generated through cooperative anti-predator behaviours, predator dilution, or exploitation [29].

Using the transformation $x = \frac{c}{\alpha}u$, $y = \frac{c}{\beta}v$ and $dt = \frac{1}{c}d\tau$, the system (1) can be rewritten as follows:

$$
\begin{aligned}
\frac{du}{d\tau} &= a_1u + a_2u^2 - a_3u^3 - kuv, \\
\frac{dv}{d\tau} &= -v + uv - v^2,
\end{aligned}
\tag{2}
$$

where $a_1 = \frac{b_1}{c}$, $a_2 = \frac{b_2}{\alpha}$, $a_3 = \frac{b_3c}{\alpha^2}$ and $k = \frac{b_4}{\beta}$.

Huang *et al.* [20] investigated uniqueness conditions and the relative positions of limit cycles solutions for (2). Huang *et al.* [21] also studied the conditions for the existence of multiple limit cycles. Bie [30] introduced diffusion in (2), and investigated the global existence of constant steady states. He also established the conditions for the existence and non-existence of non-constant stationary solutions, using the energy method. Wang [31] used a Lyapunov function to prove the global stability of the positive steady state. Moreover, he illustrated numerically, how the diffusion of predators affects the pattern dynamics.

It is observed that animals in nature move in groups or bands [32]. Studying the dynamic of each band of species in an ecological system, can help to understand the overall dynamic of the system. Mathematically, travelling wave solutions are employed to describe the bands behaviour and the mass motion. In cell biology, bands have been used to describe the aggregation of bacteria via chemotaxis [33–37]. They have also been used to understand and control wound healing processes through the collective motion of cells [38–40]. In ecology, travelling wave solutions have been used to study the swarming behaviour of insects [8]. They have been used less to study the dynamics in other classes of animals (such as mammals, *etc.*), and their interaction with their environment. This is due to the fact that the distribution of the travelling wave solutions is usually interpreted as a dispersion.

In this work, we contribute to understanding the dynamics of predator-prey model with cubic growth. We focus on each band of players in the system, and we specifically investi-

gate their asymptotic behaviour (mainly the temporal change) via a travelling waves analysis. We also examine the effects of the interactions between the prey and the predators on the ecological system. More importantly, we account for the individual behaviour of each player of the system, by introducing a velocity to each players movement. We investigate the impact of the microscale parameters (representing individual behaviour) on the behaviour of the bands. From a band point of view, we consider the diffusion to describe the spatial distribution. We illustrate the types of patterns (resulting from the transport-driven instability) that can be observed in our models.

2 Preliminary results

The system (2) has two steady states $D_0 = (0,0)$ and $D_1 = (u_1, 0)$, and another (positive) steady state $D_2 = (u^*, v^*)$ if $a_3 < a_1 + a_2$, where

$$u_1 = \frac{a_2 + \sqrt{a_2^2 + 4a_3 a_1}}{2a_3}, \qquad u^* = \frac{a_2 - k + \sqrt{(a_2 - k)^2 + 4a_3(a_1 + k)}}{2a_3},$$

$$v^* = u^* - 1. \tag{3}$$

The stability analysis of (2) is given in the following theorem [25, 30].

Theorem 2.1

   (i) *The trivial steady state D_0 is a saddle point.*
  (ii) *The steady state D_1 is globally stable if $a_1 + a_2 \leq a_3$, and a saddle point otherwise.*
 (iii) *For $a_3 < a_1 + a_2$, the positive steady state D_2 is stable if $p < 0$, and unstable if $p > 0$, where $p = (-1 - a_2 + 2k)u^* + (1 - 2a_2 - 2k)$.*

3 Microscale analysis driven by transport

Here, we investigate, from an individual perspective, the formation and behaviour of bands of animals in a predator-prey model, via the study of the travelling wave solutions. To represent the movement, we introduce a velocity for each player in the system. Our model is given by

$$\frac{\partial u}{\partial t} + s_1 . \nabla u = a_1 u + a_2 u^2 - a_3 u^3 - kuv,$$

$$\frac{\partial v}{\partial t} + s_2 . \nabla v = -v + uv - v^2, \tag{4}$$

where $u(r,t)$ and $v(r,t)$ are, respectively, the densities of prey and predator population at the position $r = (x,y)$ and time t. The operator $\nabla = (\partial/\partial x, \partial/\partial y)$, the parameters $s_1 = (s_1^1, s_1^2)$ and $s_2 = (s_2^1, s_2^2)$ are the average velocity of each (individual) prey and predator, respectively, the coefficients a_1, a_3 and k are positive, and a_2 is arbitrary.

We consider the following invariants for the travelling wave analysis:

$$z = -\kappa . r + ct, \qquad u(x,t) = U(z), \qquad v(x,t) = V(z), \tag{5}$$

where $\kappa = (\kappa_1, \kappa_2)$ is the wave vector, and c is the wave speed. Then (4) becomes

$$(c - \kappa . s_1)U' = a_1 U + a_2 U^2 - a_3 U^3 - kUV,$$

$$(c - \kappa . s_2)V' = -V + UV - V^2, \tag{6}$$

where the superscript $'$ represents the total derivative with respect to z. We note that the formation of bands in the model (4) is equivalent to demonstrating the existence of the converging travelling wave solutions $U(z)$ and $V(z)$. The travelling wave solutions $U(z)$ can be interpreted as the density of the band of prey moving with the speed c, and $V(z)$ the density of the band of predator catching the prey at the speed c. We note that the steady states D_0, D_1 and D_2 introduced in Section 2 are also steady states of (4) and (6).

Theorem 3.1

(i) *The trivial steady state D_0 is stable if $\kappa.s_2 < c$ and $c < \kappa.s_1$, and unstable otherwise.*

(ii) *The steady state D_1 is stable if $c > \max(\kappa.s_1, \kappa.s_2)$ and $a_1 + a_2 \leq a_3$, or $\kappa.s_1 < c < \kappa.s_2$ and $a_3 < a_1 + a_2$, and unstable otherwise.*

(iii) *For $a_3 < a_1 + a_2$, the positive steady state D_2 is stable if $p_1 < 0$ and either $c < \min(\kappa.s_1, \kappa.s_2)$, or $c > \max(\kappa.s_1, \kappa.s_2)$, and unstable otherwise, where $p_1 = \alpha_2/(c - k.s_2) - v^*/(c - k.s_2)$, and $\alpha_2 = -2(a_1 + k) + (2k - a_2)u^*$.*

Proof When $c > \max(\kappa.s_1, \kappa.s_2)$, the systems (2) and (6) behave the same asymptotically in the vicinity of the steady states (we note that the eigenvalues of the Jacobian matrix to (6) evaluated at the steady state are the product of $(c - \kappa.s_i)^{-1}$, which is positive, and the eigenvalues of (2) at that steady state). As a result, the stability analysis in Theorem 2.1 applies.

Now we assume $c < \kappa.s_1$ or $c < \kappa.s_2$.

In the vicinity of D_0, the Jacobian matrix is given by

$$J_{D_0} = \begin{pmatrix} \frac{a_1}{c - \kappa.s_1} & 0 \\ 0 & \frac{-1}{c - \kappa.s_2} \end{pmatrix}. \tag{7}$$

For $c < \kappa.s_2$ or $c > \kappa.s_1$, D_0 is unstable (since at least one eigenvalue will be positive). However, for $c > \kappa.s_2$ and $c < \kappa.s_1$, the steady state D_0 is stable.

In the vicinity of D_1, the Jacobian matrix is given by

$$J_{D_1} = \begin{pmatrix} \frac{-\alpha_1}{c - \kappa.s_1} & \frac{-ku_1}{c - \kappa.s_1} \\ 0 & \frac{u_1 - 1}{c - \kappa.s_2} \end{pmatrix}, \tag{8}$$

where $\alpha_1 = -a_1 - 2a_2u_1 + 3a_3u_1^2 > 0$. The determinant and the trace of J_{D_1} are given by

$$\Delta_1 = \frac{-\alpha_1(u_1 - 1)}{(c - \kappa.s_1)(c - \kappa.s_2)}, \qquad \tau_1 = \frac{-\alpha_1}{c - \kappa.s_1} + \frac{u_1 - 1}{c - \kappa.s_2}. \tag{9}$$

For $c < \min(\kappa.s_1, \kappa.s_2)$ or $\kappa.s_2 < c < \kappa.s_1$, the steady state D_1 is unstable (since either $\Delta_1 < 0$ or $\tau_1 > 0$). However, for $\kappa.s_1 < c$ and $c < \kappa.s_2$, the steady state D_1 is stable if $u_1 > 1$ (*i.e.*, $a_3 < a_1 + a_2$), and unstable if $u_1 < 1$.

In the vicinity of D_2, the Jacobian matrix is given by

$$J_{D_2} = \begin{pmatrix} \frac{\alpha_2}{c - \kappa.s_1} & \frac{-ku^*}{c - \kappa.s_1} \\ \frac{v^*}{c - \kappa.s_2} & -\frac{v^*}{c - \kappa.s_2} \end{pmatrix}, \tag{10}$$

where $\alpha_2 = a_1 + 2a_2 u^* - 3a_3(u^*)^2 - kv^* = -2(a_1 + k) + (2k - a_2)u^*$. The determinant and the trace of J_{D_2} are given by
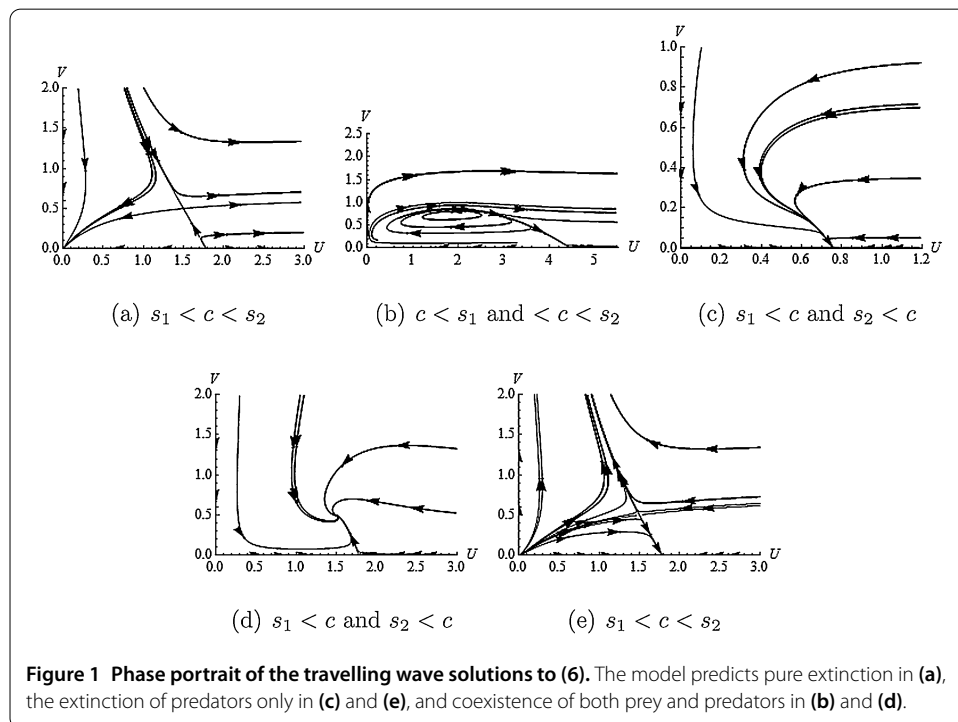
$$\Delta_2 = \frac{v^*(ku^* - \alpha_2)}{(c - \kappa.s_1)(c - \kappa.s_2)}, \qquad \tau_1 = p_1 = \frac{\alpha_2}{c - \kappa.s_1} - \frac{v^*}{c - \kappa.s_2}, \tag{11}$$

respectively. We note that $ku^* - \alpha_2 > 0$.

If $\kappa.s_1 < c < \kappa.s_2$ or $\kappa.s_2 < c < \kappa.s_1$, then $\Delta_2 < 0$ and D_2 is unstable. For $c < \min(\kappa.s_1, \kappa.s_2)$, the steady state D_2 is stable if $p_1 < 0$, and unstable if $p_1 > 0$. □

To simplify an understanding and interpretation of results from Theorem 3.1, we consider one dimensional space and we scale κ to one. Then s_1 and s_2 are the average speed of each individual prey and predator, respectively. We define slow movement as the case where the speed at which a band of prey moves is less than the average speed of each prey (*i.e.*, $c < s_1$), and fast movement otherwise. We also define weak predation as the situation where the speed at which a band of predator catches a prey is less than the average speed of each predator (*i.e.*, $c < s_2$), and strong predation otherwise. We note that the solutions behave the same as $z \to \infty$ or as $t \to \infty$.

From Theorem 3.1, we observe in the case of slow movement and strong predation ($c < s_1$ and $c > s_2$), the possibility of pure extinction (of both prey and predators) in the system. This situation can occur when the prey are less sensitive to the predators. They are under no pressure ($c < s_1$) and are less interested in their security. However, hungry predators move rapidly ($c > s_2$). As a result, predators catch prey and deplete them all in time, starve and die off. This justifies the stability of the steady state D_0 in this scenario. An illustration of the phase portrait can be seen in Figure 1(a) (we set $a_1 = 1$, $a_2 = 3$, $a_3 = 2$, $k = 2$, $c = 40$, $s_1 = 60$, $s_2 = 20$).

Figure 1 Phase portrait of the travelling wave solutions to (6). The model predicts pure extinction in **(a)**, the extinction of predators only in **(c)** and **(e)**, and coexistence of both prey and predators in **(b)** and **(d)**.

In the case of slow movement and weak predation ($c < s_1$ and $c < s_2$), we observe coexistence of both predators and prey in the system (since D_2 is the only stable steady state in this situation). Here, predators are satiated and under no environmental influence (such as hunting, extreme weather conditions, *etc.*), and prey are not too sensitive to the presence of predators. The prey population cannot become extinct as they (individually) can run at a speed faster than they can be caught ($c < s_1$). The phase portrait of the solutions in this case are illustrated in Figure 1(b) (we set $a_1 = 0.1$, $a_2 = 0.2$, $a_3 = 0.05$, $k = 0.4$, $c = 10$, $s_1 = 12$, $s_2 = 95$).

In the case of fast movement and strong predation ($c > s_1$ and $c > s_2$), D_1 and D_2 are the only possible stable steady states of the system. Here, predators and prey can be under environmental influence (such as hunting, predation, extreme weather conditions, *etc.*) to move rapidly. When they are more concerned in movement than consumption, they die off as time goes on. As a result, the prey population will reach a certain capacity in the absence of predators. This justifies the stability of D_1. However, when predators are more interested in consumption than movement, coexistence of both predators and prey can be observed in the system. An illustration of the phase portrait of the solutions are given in Figure 1(c) (here $a_1 = 1$, $a_2 = 0.2$, $a_3 = 2$, $k = 2$, $c = 80$, $s_1 = 60$, $s_2 = 20$) and Figure 1(d) (here $a_1 = 1$, $a_2 = 3$, $a_3 = 2$, $k = 2$, $c = 80$, $s_1 = 10$, $s_2 = 60$).

In the case of fast movement and weak predation ($c > s_1$ and $c < s_2$), provided $a_3 < a_1 + a_2$, D_1 is the only stable steady state. This scenario could occur when predators are in a survival mode (due to hunting, extreme weather conditions, lack of water, infection by an epidemic *etc.*). They are less interested in food. As time goes on, they become extinct. As a result, prey freely grow until they reach saturation. We illustrate the phase portrait of the solutions in Figure 1(e) (here $a_1 = 1$, $a_2 = 3$, $a_3 = 2$, $k = 2$, $c = 40$, $s_1 = 10$, $s_2 = 60$).

4 Macroscale analysis driven by diffusion

In this section, we approach the problem from a band (and population) point of view. We assume that each band of prey and predator diffuse at constant rates d_1 and d_2, respectively. The diffusion model is given by

$$
\begin{aligned}
\frac{\partial u}{\partial t} &= a_1 u + a_2 u^2 - a_3 u^3 - kuv + d_1 \nabla^2 u, \\
\frac{\partial v}{\partial t} &= -v + uv - v^2 + d_2 \nabla^2 v,
\end{aligned}
\tag{12}
$$

where $u(r, t)$ and $v(r, t)$ are, respectively, the densities of prey and predator population at the position $r = (x, y)$ and time t, and $\nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}$.

Again we consider the invariants:

$$
z = -\kappa.r + ct, \qquad u(x, t) = U(z), \qquad v(x, t) = V(z).
\tag{13}
$$

Then (12) can be reduced to

$$
\begin{aligned}
cU' &= a_1 U + a_2 U^2 - a_3 U^3 - kUV + \delta_1 U'', \\
cV' &= -V + UV - V^2 + \delta_2 V'',
\end{aligned}
\tag{14}
$$

where the superscript $'$ represents the total derivative with respect to z, $\kappa = (\kappa_1, \kappa_2)$ is the wave vector, c is the wave speed, and $\delta_1 = d_1 \kappa^2$ and $\delta_2 = d_2 \kappa^2$.

Setting

$$U_1 = U' \quad \text{and} \quad V_1 = V', \tag{15}$$

then (14) can be rewritten as follows:

$$\begin{pmatrix} U \\ U_1 \\ V \\ V_1 \end{pmatrix}' = \begin{pmatrix} U_1 \\ -\frac{a_1}{\delta_1} U - \frac{a_2}{\delta_1} U^2 + \frac{a_3}{\delta_1} U^3 + \frac{k}{\delta_1} UV + \frac{c}{\delta_1} U_1 \\ V_1 \\ \frac{1}{\delta_2} V - \frac{1}{\delta_2} UV + \frac{1}{\delta_2} V^2 + \frac{c}{\delta_2} V_1 \end{pmatrix}, \tag{16}$$

and admits $G_0 = (0,0,0,0)$, $G_1 = (u_1, 0, 0, 0)$ and $G_2 = (u^*, 0, v^*, 0)$ as steady states, where u_1, u^* and v^* are given in (3). We note that the non-negative steady state G_2 exists if $a_3 < a_1 + a_2$.

Theorem 4.1 *The three constant steady states G_0, G_1 and G_2 are unstable.*

Proof In the vicinity of G_0, the Jacobian matrix of the system (16) evaluated at G_0 is given by

$$J_{G_0} = \left(\begin{array}{cc|cc} 0 & 1 & 0 & 0 \\ \frac{-a_1}{\delta_1} & \frac{c}{\delta_1} & 0 & 0 \\ \hline 0 & 0 & 0 & 1 \\ 0 & 0 & \frac{1}{\delta_2} & \frac{c}{\delta_2} \end{array} \right), \tag{17}$$

and the associated eigenvalues to J_{G_0} are given by

$$\lambda_{1,2} = \frac{c \mp \sqrt{c^2 - 4a_1\delta_1}}{2\delta_1}, \qquad \lambda_{3,4} = \frac{c \mp \sqrt{c^2 + 4\delta_2}}{2\delta_2}. \tag{18}$$

Since $\lambda_3 > 0$ and $\lambda_4 > 0$, then the trivial steady state G_0 is unstable. Moreover, it is an unstable node given that $\Re(\lambda_2) > 0$.

In the vicinity of G_1, the Jacobian matrix is given by

$$J_{G_1} = \left(\begin{array}{cc|cc} 0 & 1 & 0 & 0 \\ \frac{\alpha_1}{\delta_1} & \frac{c}{\delta_1} & \frac{ku_1}{\delta_1} & 0 \\ \hline 0 & 0 & 0 & 1 \\ 0 & 0 & \frac{1-u_1}{\delta_2} & \frac{c}{\delta_2} \end{array} \right), \tag{19}$$

where $\alpha_1 = -a_1 - 2a_2u_1 + 3a_3u_1^2 > 0$, and the corresponding eigenvalues are given by

$$\lambda_{1,2} = \frac{c \mp \sqrt{c^2 + 4\alpha_1\delta_1}}{2\delta_1}, \qquad \lambda_{3,4} = \frac{c \mp \sqrt{c^2 + 4\delta_2(1 - u_1)}}{2\delta_2}. \tag{20}$$

Clearly, the steady state G_1 is unstable.

In the vicinity of G_2, the Jacobian matrix and its determinant evaluated at G_2 are, respectively, given by

$$J_{G_2} = \begin{pmatrix} 0 & 1 & 0 & 0 \\ \frac{\alpha_2}{\delta_1} & \frac{c}{\delta_1} & \frac{ku^*}{\delta_1} & 0 \\ 0 & 0 & 0 & 1 \\ \frac{-\nu^*}{\delta_2} & 0 & \frac{\nu^*}{\delta_2} & \frac{c}{\delta_2} \end{pmatrix}, \quad \text{and} \quad \Delta_{G_2} = \frac{\nu^*(ku^* + \alpha_2)}{\delta_1 \delta_2} > 0, \tag{21}$$

where $\alpha_2 = -a_1 - 2a_2 u^* + 3a_3(u^*)^2 + k\nu^*$. The characteristic polynomial associated to J_{G_2} is given by

$$p(\lambda) = \lambda^4 + a_3 \lambda^3 + a_2 \lambda^2 + a_1 \lambda + a_0, \tag{22}$$

where $a_3 = -c(\delta_1 + \delta_2)/(\delta_1 \delta_2)$, $a_2 = (c^2 - \delta_1 \nu^* - \delta_2 \alpha_2)/(\delta_1 \delta_2)$, $a_1 = c(\nu^* + \alpha_2)/(\delta_1 \delta_2)$ and $\alpha_0 = \Delta_{G_2}$. Since $a_3 < 0$, from the Routh-Hurwitz criterion for stability [41], the positive steady state G_2 is unstable. $\qquad \square$

Unlike the results in Theorem 2.1 and Theorem 3.1, we observe in Theorem 4.1 using the invariants (13) that diffusion creates instability in the system. However, looking from a population perspective, if we assume that the solutions of (12) are separable and of the form

$$u(x, y, t) = A(t)e^{j(\kappa_1 x + \kappa_2 y)}, \qquad \nu(x, y, t) = B(t)e^{j(\kappa_1 x + \kappa_2 y)}, \tag{23}$$

then

$$\nabla^2 u = -\kappa^2 u, \qquad \nabla^2 \nu = -\kappa^2 \nu. \tag{24}$$

As a result, (12) can be reduced to the following differential equations:

$$\begin{aligned} \frac{\partial u}{\partial t} &= (a_1 - d_1 \kappa^2)u + a_2 u^2 - a_3 u^3 - ku\nu, \\ \frac{\partial \nu}{\partial t} &= -(1 + d_2 \kappa^2)\nu + u\nu - \nu^2. \end{aligned} \tag{25}$$

For $a_1 < d_1 \kappa^2$, the trivial steady state D_0 is stable. Likewise it can be shown that the steady states D_1 and D_2 can be stable. Therefore, the presence of diffusion can stabilise the system (or conserve the stability), or can destabilise the system. This type of multi-dynamics is most often observed in models employing partial differential equations (PDEs). PDEs with the same initials conditions can have different solutions resulting to different behaviours, dependent on the type of invariants employed.

5 Pattern formation

In this section, numerical simulations are made to illustrate patterns that can be observed in the models. We used the Exponential Time Differencing (ETD) Euler Method for the discretisation in time (with the exponential five Runge-Kutta scheme of stiff order for been used in the computation). We also used the Pseudospectral discretisation in space. We

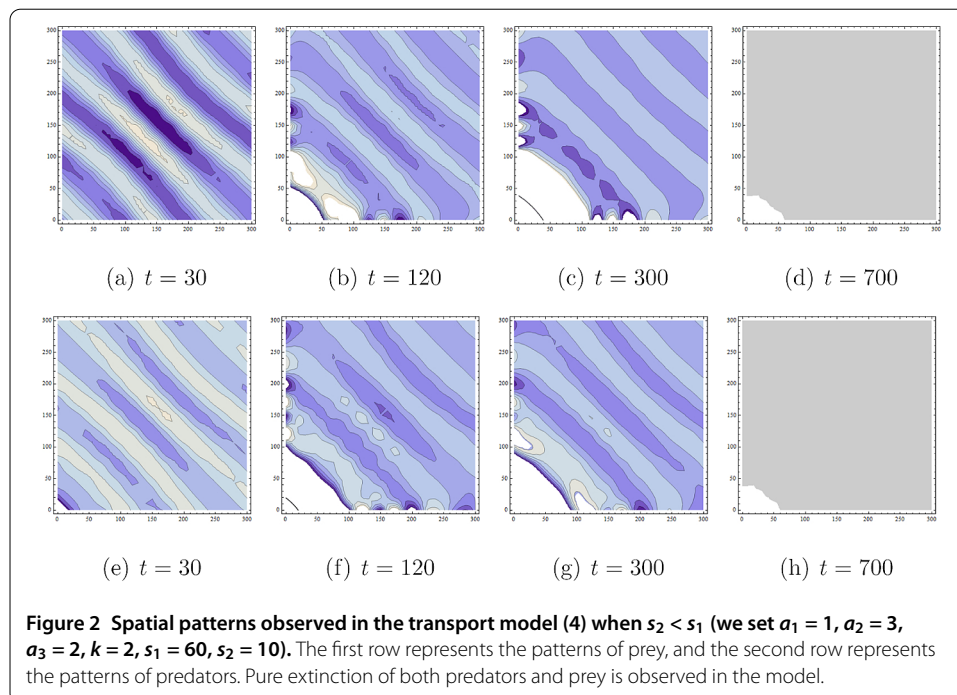considered a bounded subset of $\mathbb{R}^2$ as our spatial domain, and Dirichlet boundary conditions.

From the stability analysis in Theorem 4.1, the presence of the diffusion played a destabilizing role in the system. A Turing instability can be observed in this situation generating the formation of patterns [31, 42]. We will focus here on the transport model (4).
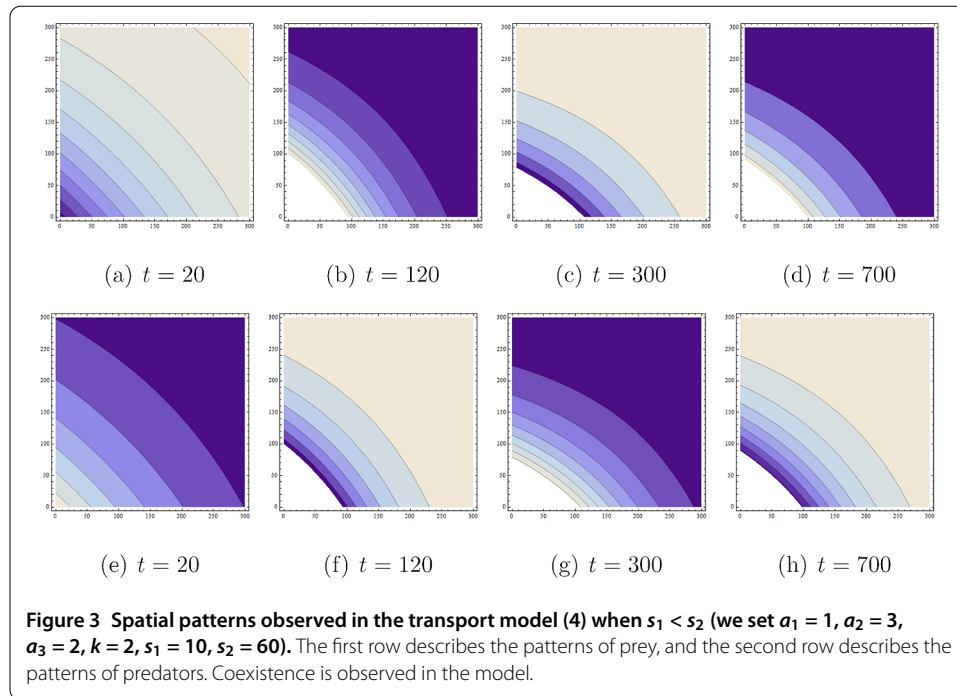
In contrast to the results obtained in the non-spatial model (2) (refer to Theorem 2.1, with $a_1 + a_2 \le a_3$), the steady state D_1 becomes unstable if the transport parameters are such that $c < \kappa.s_1$ or $c < \kappa.s_2$. Likewise, when $a_3 < a_1 + a_2$ and $p < 0$, the positive steady state D_2 becomes unstable in the presence of transport for $\kappa.s_1 < c < \kappa.s_2$ or $\kappa.s_2 < c < \kappa.s_1$. Thus, an analogous phenomenon to that of Turing instability, caused here by transport, can be observed in the model (4), and also generates the formation of patterns. This phenomenon has been labelled by Tchepmo Djomegni *et al.* [43] transport-driven instability and the general conditions for transport-driven instability are presented in that paper. There transport-driven instability is defined as a situation in which a stable steady state in the absence of a spatial distribution becomes unstable when transport is introduced in the model. An illustration of the types of patterns formed using the model (4) can be seen in Figure 2 and Figure 3.

Of interest is the fact that, while for $s_2 < s_1$ extinction is possible (see Figure 2(a)-(h)), for $s_2 > s_1$ cycles and coexistence are possible (see Figures 3(a)-(h)). These cycles also introduce patterns of differing densities of prey and predator.

6 Conclusion

In this study, the dynamics for predator-prey models with a cubic growth rate are considered with animal movement introduced to the system. The behaviour of bands of animals in the system and interplay between the bands are examined using a travelling wave analysis. Travelling wave analyses have been less exploited to describe the dynamics of ecosys-

(a) $t = 30$ (b) $t = 120$ (c) $t = 300$ (d) $t = 700$

(e) $t = 30$ (f) $t = 120$ (g) $t = 300$ (h) $t = 700$

Figure 2 Spatial patterns observed in the transport model (4) when $s_2 < s_1$ (we set $a_1 = 1$, $a_2 = 3$, $a_3 = 2$, $k = 2$, $s_1 = 60$, $s_2 = 10$). The first row represents the patterns of prey, and the second row represents the patterns of predators. Pure extinction of both predators and prey is observed in the model.

Figure 3 Spatial patterns observed in the transport model (4) when $s_1 < s_2$ (we set $a_1 = 1$, $a_2 = 3$, $a_3 = 2$, $k = 2$, $s_1 = 10$, $s_2 = 60$). The first row describes the patterns of prey, and the second row describes the patterns of predators. Coexistence is observed in the model.

tems because they are seen as representing spatial distribution studies, which physically depicts dispersion rather than groupings (or gatherings). While real ecological systems are unlikely to display simple density wave bands, as described here, our analyses illustrate how this approach can be used to consider the formation of density patterns. At this first approximation (bands of movement) we show how ecosystem stability can be dependent on animal movement velocities. We also show how density patterns can form in the presence of different movement velocities.

Unlike previous approaches, we used travelling wave invariants to describe the time distribution of the bands of animals in the system. From a local point of view, we accounted for the average individual speed of each predator and prey. We looked at the influence of individual behaviours on the collective behaviour of the bands. We also proved the existence of the travelling wave solutions, which justifies the formation of bands in the model. From a global point of view, we found that diffusion can create instability of the bands but conserve the stability of the population as a whole. This is also observed in populations of insects and flies in which the dispersion (coming in and out) can characterise (local) instability of bands [8]. However, the global movement is synchronised. We also illustrate the patterns formed using our spatial models.

In contrast to the previous findings [21, 30, 31], we show the important (and sufficient) role that transport parameters s_1, s_2 and c play in the preservation of species in the ecosystem. For instance, we predict the possibility of pure extinction in the case of slow movement of prey ($c < s_1$) and strong predation ($c > s_2$). Then over time all prey will be depleted by the predators, which in turn will starve and die.

Overall, this study shows the importance of considering individual behaviour such as movement. It also shows how sustainable ecosystems could manipulate their movement characteristics to remain stable and viable. In other words, the different species have evolved movement and predation strategies that enable co-dependent stable interactions.

It also points to management strategies that should take movements into account. For example, game sanctuaries and reserves need to be large enough for the particular predators and prey to have movement characteristics that enable sustainability. Where the reserve is too small, strong predation and relatively slow movement of prey (or not being able to escape) might occur and, as predicted, prey and predators could die out. The models developed here could be extended to help with predictions of actual reserves and help management practices. For future work, we will consider a food chain in the ecology and we will explicitly incorporate some external factors (such as logistics, weather, or resource). However, the importance of considering the individual movement strategies of animals for understanding ecosystem dynamics is highlighted here.

Competing interests
The authors declare that they have no competing interests.

Authors' contributions
All authors contributed equally to the manuscript. All authors read and approved the final manuscript.

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References
1. Malthus, TR: an Essay on the Principle of Population. Oxford World's Classics Reprint (1978) Chapter V
2. Turchin, P: Does population ecology have general laws? Oikos **94**, 17-26 (2001)
3. Verhulst, PF: Notice sur la loi que la population poursuit dans son accroissement. Correspondance mathématique et physique **10**, 113-121 (1838)
4. Banerjee, M, Abbas, S: Existence and non-existence of spatial patterns in a ratio-dependent predator-prey model. Ecol. Complex. **21**, 199-214 (2015)
5. Flores, JD, González-Olivares, E: Dynamics of a predator-prey model with Allee effect on prey and ratio-dependent functional response. Ecol. Complex. **18**, 59-66 (2014)
6. Ghorai, S, Poria, S: Turing patterns induced by cross-diffusion in a predator-prey system in presence of habitat complexity. Chaos Solitons Fractals **91**, 421-429 (2016)
7. Ghorai, S, Poria, S: Pattern formation and control of spatiotemporal chaos in a reaction diffusion prey-predator system supplying additional food. Chaos Solitons Fractals **85**, 57-67 (2016)
8. Edelstein-Keshet, L, Watmough, J, Grunbaum, D: Do travelling band solutions describe cohesive swarms? An investigation for migratory locusts. J. Math. Biol. **36**, 515-549 (1998)
9. Molina, M, Moreno-Armendáriz, M, Mora, J: Analyzing the spatial dynamics of a prey-predator lattice model with social behavior. Ecol. Complex. **22**, 192-202 (2015)
10. Sun, GQ, Jin, Z, Liu, QX: Dynamical complexity of a spatial predator-prey model with migration. Ecol. Model. **219**, 248-255 (2008)
11. Sahoo, B, Poria, S: Disease control in a food chain model supplying alternative food. Appl. Math. Model. **37**, 5653-5663 (2013)
12. ODPM (Office of the Deputy Prime Minister): The Impact of Overcrowding on Health and Education: A Review of Evidence and Literature. ODPM, London (2004)
13. Poltronieri, C, Laurà, R, Bertotto, D, Negrato, E, Simontacchi, C, Guerrera, M, Radaelli, G: Effects of exposure to overcrowding on rodlet cells of the teleost fish *Dicentrarchus labrax* (L.). Vet. Res. Commun. **33**, 619-629 (2009)
14. Kuno, E: Mathematical models for predator-prey interaction. Adv. Ecol. Res. **16**, 252-265 (1987)
15. Shen, C, Shen, BQ: A necessary and sufficient condition of the existence and uniqueness of the limit cycle for a class of prey-predator systems with sparse effect. J. Biomath. **18**, 207-210 (2003)
16. Ye, YQ, Wang, SL, Yang, XA: Theory of Limit Cycles. Am. Math. Soc., Providence (1986)
17. Zheng, J, Yu, Z, Sun, J: Existence and uniqueness of limit cycle for prey-predator system with sparse effect. J. Biomath. **16**, 156-161 (2001)
18. Biswas, D, Poria, S, Patra, SN: Phenomenological approach to describe oscillatory growth or decay in different dynamical systems. Indian J. Phys. (2016). doi:10.1007/s12648-016-0884-z
19. Biswas, D, Poria, S: Phenomenological approach for describing environment dependent growths. arXiv:1412.6939
20. Huang, X, Wang, Y, Cheng, A: Limit cycles in a cubic predator-prey differential system. J. Korean Math. Soc. **43**, 829-843 (2006)
21. Huang, X, Wang, Y, Zhu, L: I: One and three limit cycles in a cubic predator-prey system. Math. Methods Appl. Sci. **30**, 501-511 (2007)

22. Lewis, MA, Kareiva, P: Allee dynamics and the spread of invading organisms. Theor. Popul. Biol. **43**, 141-158 (1933)
23. Owen, MR, Lewis, MA: How predation can slow, stop or reverse a prey invasion. Bull. Math. Biol. **63**, 655-684 (2001)
24. Petrovskii, S, Malchow, H, Li, B: An exact solution of a diffusive predator-prey system. Proc. R. Soc. A **461**, 1029-1053 (2005)
25. Wang, MH, Kot, M: Speeds of invasion in a model with strong or weak Allee effects. Math. Biosci. **171**, 83-97 (2001)
26. Courchamp, F, Berec, L, Gascoigne, J: Allee Effects in Ecology and Conservation. Oxford University Press, London (2008)
27. Drake, JM, Kramer, AM: Allee effects. Nat. Educ. Knowl. **3**(10), 2 (2011)
28. Stephens, PA, Sutherland, WJ: Consequences of the Allee effect for behaviour, ecology and conservation. Trends Ecol. Evol. **14**, 401-405 (1999)
29. Berec, L, Angulo, E, Courchamp, F: Multiple Allee effects and population management. Trends Ecol. Evol. **22**, 185-191 (2007)
30. Bie, Q: Qualitative analysis on a cubic predator-prey system with diffusion. Electron. J. Qual. Theory Differ. Equ. **26**, 15 (2011)
31. Wang, C: Rich dynamics of a predator-prey model with spatial motion. Appl. Math. Comput. **260**, 1-9 (2015)
32. Sumpter, DJ: The principles of collective animal behaviour. Phil. Trans. R. Soc. B **361**, 5-22 (2006)
33. Tchepmo Djomegni, PM, Govinder, KS: Generalized travelling waves solutions for hyperbolic chemotaxis PDEs. Appl. Math. Model. **40**, 5672-5688 (2016)
34. Franz, B, Xue, C, Painter, K, Erban, R: Travelling waves in hybrid chemotaxis models. Bull. Math. Biol. **76**, 377-400 (2014)
35. Lapidus, IR, Schiller, R: A model for travelling bands of chemotactic bacteria. Biophys. J. **22**, 1-13 (1978)
36. Lauffenburger, DA, Kennedy, CR, Aris, R: Travelling bands of chemotactic bacteria in the context of population growth. Bull. Math. Biol. **46**, 19-40 (1984)
37. Keller, EF, Segel, LA: Travelling bands of chemotactic bacteria: a theoretical analysis. J. Theor. Biol. **30**, 235-248 (1971)
38. Dale, P, Olsen, L, Maini, PK, Sherratt, JA: Travelling waves in wound healing. Forma **10**, 205-222 (1995)
39. Landman, KA, Cai, AQ, Hughes, BD: Travelling waves of attached and detached cells in a wound-healing cell migration assay. Bull. Math. Biol. **69**, 2119-2138 (2007)
40. Maini, PK, McElwain, DL, Leavesley, D: Travelling waves in a wound healing assay. Appl. Math. Lett. **17**, 575-580 (2004)
41. Brauer, F, Nohel, JA: The Qualitative Theory of Ordinary Differential Equations: An Introduction. Dover, New York (1989)
42. Murray, JD: Mathematical Biology II: Spatial Models and Biomedical Applications. Springer, Berlin (2003)
43. Tchepmo Djomegni, PM, Collins, OC, Govinder, KS, Duffy, KJ: Investigating travelling band behaviour and pattern formation in an ecological model with transport. Preprint. University of KwaZulu-Natal (2016)