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Research Article

The "Destabilizing" Effect of Cannibalism in a Spatially Explicit Three-Species Age Structured Predator-Prey Model

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Cannibalism, the act of killing and consumption of conspecifics, is generally considered to be a stabilising process in ODE models of predator-prey systems. On the other hand, Sun et al. were the first to show that cannibalism can cause Turing instability, in the classical Rosenzweig-McArthur two-species PDE model, which is an impossibility without cannibalism. Magnússon's classic work is the first to show that cannibalism in a structured three-species predator-prey ODE model can actually be destabilising. In the current manuscript we consider the PDE form of the three-species model proposed in Magnússon's classic work. We prove that, in the absence of cannibalism, Turing instability is an impossibility in this model, for *any range of parameters*. However, the *inclusion* of cannibalism can cause Turing instability. Thus, to the best of our knowledge, we report the *first* cannibalism induced Turing instability result, in spatially explicit three-species age structured predator-prey systems. We also show that, in the classical ODE model proposed by Magnússon, cannibalism can act as a life boat mechanism, *for the prey*.

1. Introduction

Background. Cannibalism is defined as the act of killing and at least partial consumption of conspecifics. It is ubiquitous in natural predator-prey communities [1] and is observed in more than 1300 species in nature [2]. It occurs as a socioanthropological as well as ecological phenomenon [3, 4], in many varied forms. For example, a sect of ascetics in Northern India, called "Aghoris," consume corpses in the belief that such ritualistic practice, or *endocannibalism*, will enable them to attain immortality [5]. Cannibalism is also rampant amongst certain insects. Many arachnid species practice *sexual cannibalism*, where the female cannibalises her mate, before, during, or after copulation. In population models, the inclusion of cannibalism can bring about interesting and sometimes counter intuitive dynamics, such as the *life boat mechanism*. Therein the act of cannibalism causes persistence in a population, otherwise doomed to go extinct [6]. The effects of climate change induced cannibalism have also been intensely investigated recently [7–9].

A detailed survey of the current and past mathematical literature on cannibalism shows that various types of predator-prey models have been investigated [6, 10–16]. Most works in the literature consider cannibalism in the predator species. However, there are a few works that involve cannibalism among prey as well [17]. In most models, cannibalism is seen to have a strong stabilising influence [11, 14]. But some works do report that it can destabilize as well [18]. Since species disperse in space in search of food, shelter, and mates and to avoid predators, spatially dispersing populations are often modeled via partial differential equations (PDE)/spatially explicit models of interacting species [19–22]. Of particular interest to many is the phenomenon of Turing instability, first introduced by Turing [23], which shows that diffusion in a system can lead to pattern forming instabilities. In the context of cannibalism, there are very few works in the literature that consider spatially explicit models and investigate Turing instability therein. Sun et al. [24] were the first to show that cannibalism in the classical diffusive Rosenzweig-McArthur model can bring about Turing patterns. This is an impossibility in the system without cannibalism. Fasani and Rinaldi [25] generalised the cannibalism term from [24] and found that cannibalism can still bring about Turing patterns.

The above models consider cannibalism amongst the predators. In [17] we found that cannibalism amongst prey can also bring about Turing patterns, in the spatially explicit Holling-Tanner model, with ratio dependent functional response.

One approach in the literature, when considering ODE models, has been to structure the predator class into adults and juveniles and allow cannibalism of the juvenile predator by the adult predator. This essentially yields a three-species age structured ODE model. The reader is referred to [12, 14, 27], and again therein cannibalism is seen to provide a stabilising influence, depending on parameter regime. However, depending on model structure and parameter regimes, cannibalism can also destabilize [1, 17, 18]. To the best of our knowledge, there is a *complete lack* of investigation of the effects of cannibalism, on the stability of spatially explicit/ PDE three-species predator-prey models, with age structure (or without).

Classical Model of Magnússon. To this end we investigate the spatially explicit version of the model first proposed in [18] by Magnússon and further analyzed by Kaewmanee et al. [26, 28]. Magnússon proposed and investigated the following structured three-species predator-prey model, where $X(t)$, $Y(t)$, and $Z(t)$ are the biomass of an adult predator, a juvenile predator, and prey, at a given time t. The interaction between these three classes is described below:

$$\frac{dX}{dt} = -M_1 X + AY + CXZ + \gamma' SXY$$

$$\frac{dY}{dt} = RX - AY - M_2 Y - SXY \qquad (1)$$

$$\frac{dZ}{dt} = TZ - UZ^2 - VXZ.$$

Essentially the predator species is structured into adults $X(t)$ and juveniles $Y(t)$, with the adult predators feeding on a prey species $Z(t)$. Note all parameters are positive constants, and the system goes along with suitable positive initial conditions. M_1 is the death rate of adult predators, M_2 is the death rate of juvenile predators, A is the growth rate of adults predators (juveniles grow into adults), R is the growth rate of juveniles due to adults, C is the predators growth rate due to preying, T is the birth rate of prey, and V is the predators attack rate on prey. S is the cannibalism rate, and γ' is the conversion efficiency of eaten juveniles into adults. For further details see [18]. Magnússon finds that, in this particular model, the effect of including cannibalism is to *destabilise* the interior equilibrium, leading to limit cycle dynamics, through a Hopf bifurcation. This result is *contrary* to many others in the literature, where cannibalism is found to be stabilising. Note one of the problematic issues in [18] is the scaling of the predator attack rate parameter, V, which scales like $V \approx 1/S$, where S is the cannibalism rate parameter. A possible reasoning here is that if $V \approx 1/S$, then $S \approx 1/V$. So if predation/attack rate on regular prey is high, or $V \gg 1$, there is almost no need for cannibalism, and $S \ll 1$. A closer examination of the model reveals two causes for concern:

(i) This scaling does not permit one to consider the limiting case of no cannibalism ($S = 0$), in a tractable way.

(ii) There is a prey free equilibrium or no "cost" to the adult as he cannibalises the juvenile.

Rescaled Model of Tang. Part of these issues was first addressed in [26], where a more refined form of scaling is introduced.

$$u^1 = \frac{V}{M_1} X,$$

$$v^1 = \frac{VA}{M_1^2} Y,$$

$$r^1 = \frac{C}{M_1} Z, \qquad (2)$$

$$\tau = \frac{M_1}{C} t,$$

where $t_1 = T/M_1$, $m = (A + M_2)/M_1$, $r = RA/M_1^2$, $u = U/C$, $\gamma = \gamma' M_1/A$, $s = S/V$.

This yields the following nondimensionalised system, with fewer parameters

$$\frac{du^1}{d\tau} = -u^1 + v^1 + u^1 r^1 + \gamma s u^1 v^1$$

$$\frac{dv^1}{d\tau} = r u^1 - m v^1 - s u^1 v^1 \qquad (3)$$

$$\frac{dr^1}{d\tau} = t_1 r^1 - u\left(r^1\right)^2 - u^1 r^1.$$

Here typically $\gamma < 1$, but not necessarily. Now the cannibalism parameter s can be followed closely. In fact one can tractably take the limit as $s \to 0$, to obtain the model without cannibalism,

$$\frac{du^1}{d\tau} = -u^1 + v^1 + u^1 r^1$$

$$\frac{dv^1}{d\tau} = r u^1 - m v^1 \qquad (4)$$

$$\frac{dr^1}{d\tau} = t_1 r^1 - u\left(r^1\right)^2 - u^1 r^1.$$

The results that Kaewmanee and Tang find are in accordance with Magnússon; that is increasing the cannibalism parameter can lead to the stable interior equilibrium losing stability, leading to limit cycle dynamics. Kaewmanee and Tang's results, unlike Magnússon, *are not limited* to the case where there is high juvenile mortality and/or low adult recruitment. However, the Hopf bifurcation analysis as worked out in [26] is *incorrect*.

Our primary contributions in the current manuscript are the following:

(i) We explore the spatially explicit forms of the models, (3) and (4), and show global existence of solutions via Theorem 2 and Corollary 3.

(ii) We show that the spatially explicit model without cannibalism *does not* possess Turing instability in *any* parameter regime via Theorem 4. However, *introducing* cannibalism can *certainly* bring about Turing instability, via Theorem 14. To the best of our knowledge, this is the *first* cannibalism induced Turing instability result, in age structured three-species PDE models.

(iii) We derive the correct form of Hopf bifurcation in the classic ODE model proposed in [18] via Theorem 15. Note again that the previous Hopf bifurcation analysis as worked out in [26] is *incorrect*.

(iv) We numerically show that cannibalism can act as a life boat mechanism in *the prey* and conjecture that it can act as a life boat mechanism in both predator and prey via Conjectures 16 and 18.

(v) We discuss ecological interpretations, based on our work.

We relegate the details of the ODE stability analysis, as well as generic Turing instability conditions, to the Appendix. Some of these are also readily available in the literature [19, 26], so they are included in the Appendix only for completeness and benefit of the reader.

2. Spatially Explicit Model

Since species disperse in space in search of food, shelter, and mates and to avoid predators, spatially dispersing populations are often modeled via partial differential equations (PDE)/spatially explicit models of interacting species [19–22]. In this section we shall investigate the effects of diffusion induced instability in the models (4) and (3). We state the form of the one-dimensional spatially explicit model with no cannibalism,

$$
\begin{aligned}
u_t^1 &= d_1 u_{xx}^1 - u^1 + v^1 + u^1 r^1 \\
v_t^1 &= d_2 v_{xx}^1 + r u^1 - m v^1 \\
r_t^1 &= d_3 r_{xx}^1 + t_1 r^1 - u \left(r^1 \right)^2 - u^1 r^1,
\end{aligned}
\tag{5}
$$

$\gamma < 1$, and our domain $\Omega = [0, \pi]$.

We prescribe Neumann boundary conditions

$$
u_x^1 = v_x^1 = r_x^1 = 0
\tag{6}
$$

and suitable positive initial conditions

$$
\begin{aligned}
u^1 (x, 0) &> 0, \\
v^1 (x, 0) &> 0, \\
r^1 (x, 0) &> 0.
\end{aligned}
\tag{7}
$$

Here $u^1(x, \cdot)$, $v^1(x, \cdot)$, $r^1(x, \cdot)$ are the concentrations/population densities of the prey, the juvenile predator, and the adult predator, at any given time t, respectively. We next state the form of the one-dimensional spatially explicit model with cannibalism

$$
u_t^1 = d_1 u_{xx}^1 - u^1 + v^1 + u^1 r^1 + \gamma s u^1 v^1
\tag{8}
$$

$$
v_t^1 = d_2 v_{xx}^1 + r u^1 - m v^1 - s u^1 v^1
\tag{9}
$$

$$
r_t^1 = d_3 r_{xx}^1 + t_1 r^1 - u \left(r^1 \right)^2 - u^1 r^1,
\tag{10}
$$

$\gamma < 1$, and our domain $\Omega = [0, \pi]$.

We prescribe Neumann boundary conditions

$$
u_x^1 = v_x^1 = r_x^1 = 0
\tag{11}
$$

and suitable positive initial conditions

$$
\begin{aligned}
u^1 (x, 0) &> 0, \\
v^1 (x, 0) &> 0, \\
r^1 (x, 0) &> 0.
\end{aligned}
\tag{12}
$$

Here $u^1(x, \cdot)$, $v^1(x, \cdot)$, $r^1(x, \cdot)$ are the concentrations/population densities of the prey, the juvenile predator, and the adult predator, at any given time t, respectively.

2.1. Functional Preliminaries and Local Solutions. We now present various function space notations and definitions that will be used frequently. The usual norms in the spaces $\mathbb{L}^p(\Omega)$, $\mathbb{L}^\infty(\Omega)$, and $\mathbb{C}(\overline{\Omega})$ are, respectively, denoted by

$$
\begin{aligned}
|u|_p^p &= \frac{1}{|\Omega|} \int_\Omega |u(x)|^p \, dx, \\
|u|_\infty &= \max_{x \in \Omega} |u(x)|.
\end{aligned}
\tag{13}
$$

It is well known that, under the "regularizing effect principle" to prove global existence of solutions to (8)–(10), [29], it suffices to derive uniform estimates on L^p, norms of the reaction terms, on $[0, T_{\max}[$, for some $p > n/2$, where n is the spatial dimension of the domain Ω, and the reaction terms in our setting are given in (8)–(10). Here $T_{\max}$ denotes the eventual blowing-up time in $\mathbb{L}^\infty(\Omega)$. The following local existence result is well known [30].

Lemma 1. *System (8)–(10) admits a unique, classical solution* (u^1, v^1, r^1) *on* $[0, T_{\max}[\times \Omega$. *If* $T_{\max} < \infty$ *then*

$$
\lim_{t \nearrow T_{\max}} \left\{ \left\| u^1 (t, \cdot) \right\|_\infty + \left\| v^1 (t, \cdot) \right\|_\infty + \left\| r^1 (t, \cdot) \right\|_\infty \right\} = \infty.
\tag{14}
$$

Proof. Since the reaction terms are continuously differentiable in the positive octant, then for any initial data in $\mathbb{C}(\overline{\Omega})$ or $\mathbb{L}^p(\Omega)$, $p \in (1, +\infty)$, it is easy to check directly their

Lipschitz continuity on bounded subsets of the domain of a fractional power of the operator $I_3(d_1, d_2, d_3)^t \Delta$, where I_3 is the three-dimensional identity matrix, Δ is the Laplacian operator, and $(\;)^t$ denotes the transposition. □

2.2. Control of Mass and $L^1(\Omega)$ Estimates. Note, in order to derive global existence via application of [29], we are required to derive uniform in time L^p estimates on the reaction terms in (8)–(10), for $p > 1/2$. We will restrict ourselves to the case $n = 1$. To this end (8) poses a difficulty via the $\gamma s u^1 v^1$ term. We proceed by multiplying (9) by γ and adding up equations (8) and (9) to yield

$$u_t^1 + \gamma v_t^1 = d_1 u_{xx}^1 + d_2 \gamma v_{xx}^1 + (r\gamma - 1) u^1 + (1 - \gamma m) v^1 + u^1 r^1. \tag{15}$$

We now define the grouped variable $W = u^1 + \gamma v^1$ and integrate the above equation in space to obtain

$$\frac{d}{dt} \int_\Omega W(x,t)\, dx$$
$$= \int_\Omega \left((r\gamma - 1) u^1 + (1 - \gamma m) v^1 + u^1 r^1 \right) dx$$
$$\leq \max \left((r\gamma - 1), (1 - \gamma m), \|r^1\|_\infty \right)$$
$$\cdot \int_\Omega \left(u^1 + v^1 \right) dx \leq C \tag{16}$$
$$\cdot \max \left((r\gamma - 1), (1 - \gamma m), \|r^1\|_\infty \right)$$
$$\cdot \int_\Omega \left(u^1 + \gamma v^1 \right) dx = C$$
$$\cdot \max \left((r\gamma - 1), (1 - \gamma m), \|r^1\|_\infty \right) \int_\Omega W(x,t)\, dx.$$

Now the uniform in time L^1 bound on W and thus on u^1, v^1 easily follows via applying Gronwall's lemma on (16), on any time interval $[0, T]$, to yield

$$\|u^1\|_{L^1(\Omega)} \leq \|u_0^1 + \gamma v_0^1\|_{L^1(\Omega)} e^{(C \max((r\gamma-1),(1-\gamma m),\|r^1\|_\infty))T}, \tag{17}$$

$$\|v^1\|_{L^1(\Omega)}$$
$$\leq \|u_0^1 + \gamma v_0^1\|_{L^1(\Omega)} \frac{1}{\gamma} e^{(C \max((r\gamma-1),(1-\gamma m),\|r^1\|_\infty))T} \tag{18}$$

with the bound depending on only the final time $t = T$. This follows as the equation for r^1 is amenable to make essentially any estimate on r^1, by comparing it to the diffusive logistic equation. We now deal with the problematic term which is

the $u^1 v^1$ term. However, integrating (9) in $\Omega \times [0, T] = \Omega_T$ we obtain

$$\int_\Omega v^1(\cdot, T)\, dx + s \int_{\Omega_T} u^1 v^1\, dx\, dt$$
$$= r \int_{\Omega_T} u^1 - m \int_{\Omega_T} r v^1 + \int_\Omega v_0^1\, dx. \tag{19}$$

Thus

$$\|u^1 v^1\|_{\Omega_T} \leq \frac{r}{s} \int_{\Omega_T} u^1 + \frac{1}{s} \int_\Omega v_0^1\, dx$$
$$\leq \frac{r}{s} \int_0^T \|u_0^1 + \gamma v_0^1\|_{L^1(\Omega)} e^{(C \max((r\gamma-1),(1-\gamma m),\|r^1\|_\infty))t}\, dt$$
$$+ \frac{1}{s} \|v_0^1\|_{L^1(\Omega)} \tag{20}$$
$$= \frac{r}{s} \frac{\|u_0^1 + \gamma v_0^1\|_{L^1(\Omega)} e^{(C \max((r\gamma-1),(1-\gamma m),\|r^1\|_\infty))T}}{(C \max((r\gamma - 1), (1 - \gamma m), \|r^1\|_\infty))}$$
$$- \frac{1}{\|u_0^1 + \gamma v_0^1\|_{L^1(\Omega)}}.$$

This follows from the $L^1(\Omega)$ estimate on u^1, via (17). Thus we have $L^1(\Omega_T)$ control of the problematic nonlinearity. Thus we see we can uniformly bound all of the reaction terms in $L^1(\Omega_T)$ and by bootstrap argument then bound them uniformly in L^p to deduce global existence [29]. So we can state the following theorem.

Theorem 2. *Consider the spatially explicit three-species model with cannibalism (8)–(10), where the spatial dimension of the physical domain is $n = 1$. Solutions to this model are classical, that is, $(u^1, v^1, r^1) \in C^1(0, T; C^2(\Omega))$, and exist globally in time.*

A simple corollary to Theorem 2 can be stated concerning the model without cannibalism.

Corollary 3. *Consider the spatially explicit three-species model without cannibalism (5). Solutions to this model are classical, that is, $(u^1, v^1, r^1) \in C^1(0, T; C^2(\Omega))$, and exist globally in time.*

2.3. Nonexistence of Turing Instability in the Model without Cannibalism. We state and prove the following theorem.

Theorem 4. *Consider the three-species spatially explicit model without cannibalism (5). The spatially homogenous steady state (u_*^1, v_*^1, r_*^1) of this model cannot be driven unstable by diffusion, for any parameter regime.*

Proof. We show this directly by checking the necessary conditions for Turing instability from [19]. Note for Turing instability to occur we have certain necessary conditions on the coefficients of the characteristic polynomial, gotten by linearizing (5), around the spatially homogenous equilibrium

TABLE 1: Coefficients of cubic functions $A_1(k^2)A_2(k^2) - A_3(k^2)$ used in determining conditions for Turing instability.

Coefficient	$A_3(k^2)$	$[A_1 A_2 - A_3](k^2)$
h	$J_{11}J_{32}J_{23} + J_{12}J_{21}J_{33} - J_{11}J_{22}J_{33}$	$J_{11}J_{22}J_{33} - (J_{11} + J_{22} + J_{33})(J_{11}J_{22} - J_{12}J_{21} + J_{11}J_{33} + J_{22}J_{33} - J_{23}J_{32}) - J_{11}J_{23}J_{32} - J_{12}J_{21}J_{33}$
d	$d_1(J_{22}J_{33} - J_{32}J_{23}) + d_2 J_{11}J_{33} + d_3(J_{11}J_{22} - J_{12}J_{21})$	$d_1(2J_{11}J_{33} + 2J_{11}J_{22} + 2J_{22}J_{33} + J_{33}J_{33} + J_{22}J_{22} - J_{12}J_{21}) + d_2(2J_{22}J_{11} + 2J_{22}J_{33} + 2J_{33}J_{11} + J_{11}J_{11} + J_{33}J_{33} - J_{21}J_{12} - J_{23}J_{32}) + d_3(2J_{22}J_{11} + 2J_{22}J_{33} + 2J_{33}J_{11} + J_{11}J_{11} + J_{22}J_{22} - J_{23}J_{32})$
c	$-d_1 d_2 J_{33} - d_1 d_3 J_{22} - d_2 d_3 J_{11}$	$-J_{11}(d_2 + d_3)(2d_1 + d_2 + d_3) - J_{22}(d_1 + d_3)(d_1 + 2d_2 + d_3) - J_{33}(d_1 + d_2)(d_1 + d_2 + 2d_3)$
b	$d_1 d_2 d_3$	$(d_2 + d_3)(d_1 d_1 + d_2 d_3 + d_1 d_2 + d_1 d_3)$

(u_*^1, v_*^1, r_*^1). See the Appendix and Theorem C.1 therein. Note that the Jacobian matrix of the reaction terms of the model without cannibalism at the spatially homogenous equilibrium (u_*^1, v_*^1, r_*^1) is given by

$$J = \begin{bmatrix} -\dfrac{r}{m} & 1 & \left(-u + \dfrac{ur}{m} + t_1\right) \\ r & -m & 0 \\ -1 + \dfrac{r}{m} & 0 & -\dfrac{1}{m}u(m-r) \end{bmatrix}. \quad (21)$$

We now check the necessary conditions for Turing instability from Table 1, where we take the J_{ii} entries, from the above matrix.

We first check the coefficient c of A_3,

$$c = -\left[-d_1 d_2 u r_*^1 - d_1 d_3(m) - d_2 d_3\left(\dfrac{r}{m}\right)\right] > 0. \quad (22)$$

We next check the coefficient c of $A_1 A_2 - A_3$,

$$c = \left[\dfrac{r}{m}(d_2 + d_3)(2d_1 + d_2 + d_3) \right.$$
$$+ m(d_1 + d_3)(d_1 + 2d_2 + d_3) \quad (23)$$
$$\left. + u r_*^1(d_2 + d_1)(d_1 + d_2 + 2d_3)\right] > 0.$$

We next check the coefficient d of A_3,

$$d = d_1\left(m\left(u r_*^1\right)\right) + d_2\left(\left(r_*^1 - 1\right)\left(-u r_*^1\right) + u_*^1 r_*^1\right)$$
$$+ d_3\left(-m\left(r_*^1 - 1\right) - r\right) \quad (24)$$
$$= d_1\left(m\left(u r_*^1\right)\right) + d_2\left(\left(r_*^1 - 1\right)\left(-u r_*^1\right) + u_*^1 r_*^1\right)$$
$$> 0.$$

We next check the coefficient d of $A_1 A_2 - A_3$,

$$d = d_1\left(\dfrac{2r}{m^2}u(m-r) + r + 2u(m-r)\right.$$
$$+ \left(\dfrac{1}{m}u(m-r)\right)^2 + (m)^2 + u_*^1 r_*^1\right)$$
$$+ d_2\left(\dfrac{2r}{m^2}u(m-r) + r + 2u(m-r)\right. \quad (25)$$
$$+ \left(\dfrac{1}{m}u(m-r)\right)^2 + \left(\dfrac{r}{m}\right)^2\right) + d_3\left(\dfrac{2r}{m^2}u(m-r)\right.$$
$$+ 2r + 2u(m-r) + (m)^2 + \left(\dfrac{r}{m}\right)^2 + u_*^1 r_*^1\right) > 0.$$

Since all of these coefficients are positive, the result follows as an application of Theorem C.1 from the Appendix and simple contraposition. This proves the theorem. □

Remark 5. Note that Theorem 4 shows that there does not exist Turing instability in the model without cannibalism (5), for *any* parameter regime.

2.4. Existence of Turing Instability with Cannibalism.
Given that there is no Turing instability in the model without cannibalism (5), we now investigate the effect of including cannibalism, on Turing instability in the model. To this end we investigate the spatially explicit model (8)–(10). We first introduce several structure theorems from linear algebra in the literature [31–33].

Definition 6 (strongly stable). A real matrix A is said to be strongly stable if $A - D$ is stable for all diagonal matrices D.

Definition 7. Let P denote the class of matrices whose signed principal minors are all positive and P_0^+ the class whose signed principal minors are all nonnegative, with one of each order positive.

Theorem 8. *A 3×3 real matrix A is strongly stable if and only if $A \in P_0^+$, and A is stable.*

Theorem 9. *A is strongly stable if and only if A is s-stable.*

Theorem 10. *If the kinetic system*

$$\frac{du}{dt} = f(u, v, r)$$

$$\frac{dv}{dt} = g(u, v, r) \qquad (26)$$

$$\frac{dr}{dt} = h(u, v, r)$$

is s-stable, then no Turing bifurcation is possible from the uniform steady state solution.

Theorem 11. *If the kinetic system*

$$\frac{du}{dt} = f(u, v, r)$$

$$\frac{dv}{dt} = g(u, v, r) \qquad (27)$$

$$\frac{dr}{dt} = h(u, v, r)$$

contains an unstable subsystem, then Turing bifurcation is possible from the uniform steady state solution.

Remark 12. We will now use the above theory to show that cannibalism can in fact induce Turing instability. We will first show that the Jacobian matrix of the reaction terms of the model with cannibalism (8)–(10), given by (A.2), is *not* strongly stable, for certain values of the cannibalism parameter *s*. This will yield the result as a simple corollary to Theorems 9 and 10. Note similar ideas were used in [32], to show that a certain SEIR type epidemics model does not possess Turing instability, as long as the disease-caused death rate parameter is zero, but can have Turing patterns for positive disease-caused death rate.

Recall the Jacobian matrix of the reaction terms of the model with cannibalism is given by

$$J = \begin{bmatrix} r_*^1 - 1 + \gamma s v_*^1 & 1 + \gamma s u_*^1 & u_*^1 \\ r - s v_*^1 & -m - s u_*^1 & 0 \\ -r_*^1 & 0 & t_1 - 2u r_*^1 - u_*^1 \end{bmatrix}$$

$$= \begin{bmatrix} \text{free} & + & + \\ + & - & 0 \\ - & 0 & - \end{bmatrix}. \qquad (28)$$

Remark 13. Notice we write the sign of J_{11} as free, because due to the cannibalism parameter *s* the sign of $J_{11} = r_*^1 - 1 + \gamma s v_*^1$ could now be positive or negative.

Theorem 14. *Consider the three-species model with cannibalism (8)–(10) and its Jacobian matrix J of reaction terms, given*

by (28). Consider a parameter set for which J is stable, whilst the cannibalism parameter s satisfies

$$r_*^1 - 1 + \gamma s v_*^1 > 0,$$

$$r_*^1 - 1 + \gamma s v_*^1 - m - s u_*^1 > 0, \qquad (29)$$

$$\text{or } r_*^1 - 1 + \gamma s v_*^1 + t_1 - 2u r_*^1 - u_*^1 > 0.$$

Then there exist diffusion coefficients (d_1, d_2, d_3), such that the spatially homogenous steady state (u_*^1, v_*^1, r_*^1) of (8)–(10) can be driven unstable due to Turing instability.

The proof relies on extracting an unstable submatrix from (28). This is equivalent to some signed principal minor not belonging to P_0^+ and hence J given by (28) not being strongly stable.

Proof. Note if we look at the minor gotten by removing row 3 and column 3, we obtain the following submatrix:

$$\begin{bmatrix} r_*^1 - 1 + \gamma s v_*^1 & 1 + \gamma s u_*^1 \\ r - s v_*^1 & -m - s u_*^1 \end{bmatrix}. \qquad (30)$$

This is clearly seen to be unstable if $r_*^1 - 1 + \gamma s v_*^1 - m - s u_*^1 > 0$. Also, if we look at the minor gotten by removing row 2 and column 2, we obtain the following submatrix:

$$\begin{bmatrix} r_*^1 - 1 + \gamma s v_*^1 & u_*^1 \\ -r_*^1 & t_1 - 2u r_*^1 - u_*^1 \end{bmatrix}. \qquad (31)$$

This is clearly seen to be unstable if $r_*^1 - 1 + \gamma s v_*^1 + t_1 - 2u r_*^1 - u_*^1 > 0$.

Thus if either of these conditions are met, J given by (28) contains unstable submatrices. That is, certain signed principal minors are not in P_0^+. Thus via Theorem 8 J is not strongly stable, which implies via Theorem 9 that J is not *s*-stable. This then implies that there exist diffusion coefficients (d_1, d_2, d_3) for which Turing instability is a *certainty*, via an application of Theorems 10 and 11. This proves the theorem. □

3. Numerical Analysis of Turing Instability

3.1. The Effect of Cannibalism on Turing Instability. We now numerically demonstrate that if the conditions via Theorem 14 are met, we can find diffusion coefficients d_1, d_2, d_3 so as to induce Turing instability in (8)–(10). We choose the following parameter set, $d_1 = 10^{-11}, d_2 = 1.7 \times 10^{-8}, d_3 = 0.9, r = 0.01, m = 0.1, \gamma = 0.01, s = 0.01, u = 0.13, t_1 = 0.21$. For this parameter set we see that $u_*^1 = 0.058844, v_*^1 = 0.005850, r_*^1 = 1.162736$. Thus $r_*^1 - 1 + \gamma s v_*^1 = 0.1627 > 0$ and $r_*^1 - 1 + \gamma s v_*^1 - m - s u_*^1 = 0.0614 > 0$. Thus the conditions of Theorem 14 are met, and we can expect Turing instability. This is demonstrated in the plots next.

3.2. Sensitivity Analysis: Turing Space and Dispersion Plots. Since cannibalism is the *sole* factor in bringing about Turing

instability in (8)–(10), we decide to further investigate this result. We perform next a sensitivity analysis, also referred to as a Turing space analysis, considering the effect on Turing instability with two parameters at a time. Since cannibalism is the central theme under investigation, we check the sensitivity of the cannibalism parameter against *every* other parameter. In our simulations we refer to the current literature [8, 34] to keep the parameters close to reality. In all of the plots in Figures 2 and 3 the blue area is the region where Turing instability exists, and the white area is the region where it does not. The results are presented next.

We next display the dispersion relation, as we vary the cannibalism parameter s.

We interpret and discuss the above results in the Discussion and Conclusion (Section 6).

4. Hopf Bifurcation

4.1. Hopf Bifurcation in Terms of the Cannibalism Parameter. We will now investigate the correct criterion for Hopf bifurcation in (3), in terms of the cannibalism parameter s. The criterion provided in [26] is incorrect. See Figures 6 and 7. In order to investigate the Hopf bifurcation of model system (3), we follow the method developed by Liu [35]. It can be seen that the Hopf bifurcation at $s = s^*$ can occur provided that $A_1(s^*)$, $A_3(s^*)$, and $\Phi(s^*) = A_1(s^*)A_2(s^*) - A_3(s^*)$ are smooth functions of s in an open interval of $s \in \mathbb{R}$ such that

(1) $A_1(s^*) > 0$, $A_3(s^*) > 0$, and $\Phi(s^*) = A_1(s^*)A_2(s^*) - A_3(s^*) = 0$;

(2) $(d\Phi(s)/ds)|_{s=s^*} \neq 0$.

Thus we can state the following theorem.

Theorem 15. *Under conditions (B.2), (B.3), (B.5), (B.7), and (B.9) there is a Hopf bifurcation of the positive equilibrium point (u_*^1, v_*^1, r_*^1) at $s = s^*$ of model system (3), where $A_1(s^*) > 0$, $A_3(s^*) > 0$, and $A_1(s^*)A_2(s^*) - A_3(s^*) = 0$.*

The coefficients A_1, A_2, and A_3 and details of conditions (B.2)–(B.9) are provided in the Appendix.

We now numerically illustrate a correct bifurcation point for Hopf instability. We begin by trying to find an $s = s^*$, such that $\Phi(s^*) = A_1(s^*)A_2(s^*) - A_3(s^*) = a(s^*)^2 + bs^* + c = 0$ whilst $(d\Phi(s)/ds)|_{s=s^*} = 2as^* + b \neq 0$.

The form of Φ is complicated and depends on the correctly calculated A_1, A_2, A_3; see the Appendix. We choose the same parameters from [26], $r = 0.5$, $m = 1$, $u = 0.1$, $\gamma = 1.5$, $t_1 = 1.3$, but the correct form of the coefficients as we have worked out in the Appendix and plot $\Phi(s)$.

5. Cannibalism as a Life Boat Mechanism

Cannibalism often gives rise to counterintuitive phenomenon in population dynamics. A *life boat mechanism* is a feature of cannibalism, where a noncannibalistic population is doomed to extinction but can persist under the act of cannibalism. We now explore such features in our model systems. We first

show numerically that a life boat mechanism for the prey exists. Next we conjecture that a life boat mechanism for the predator also exists.

5.1. Cannibalism as a Life Boat for the Prey. Notice that, in the special case that $r = m$, a prey free equilibrium $(u_*^1, v_*^1, 0)$ is possible in both the no cannibalism model (4) and the model with cannibalism (3). We show in Figure 8 numerically that a life boat mechanism for the prey also exists. This is not proved rigorously. A rigorous investigation will have to employ the normal form theory, for nonlinear stability analysis, as there are two zero eigenvalues at equilibrium (u_*^1, v_*^1, r_*^1), and thus this equilibrium point is nonhyperbolic. However we can make the following conjecture.

Conjecture 16. *Consider model system (3). Under certain parametric restrictions, if there is no cannibalism, that is, $s = 0$, a small perturbation to prey free state $(u_*^1, v_*^1, 0)$ will still yield extinction of the prey. However, if $s > 0$, the prey population will recover, to reach a nontrivial (u_*^1, v_*^1, r_*^1) state.*

Remark 17. What we notice is that, under certain parametric restrictions, the prey free state is globally stable, but introducing cannibalism results in coexistence of all species, and orbits converge to a nontrivial interior equilibrium (u_*^1, v_*^1, r_*^1). This shows that a life boat mechanism exists for the prey as well. Also see Figure 8.

5.2. Cannibalism as a Life Boat for the Predator

Conjecture 18. *Consider model system (3). Under certain parametric restrictions there exist cannibalism rates γ, s such that if there is no cannibalism, that is, $s = 0$, a small perturbation to the predators in the $(0, 0, t_1/u)$ state will still yield extinction of the predator. However, if $s > 0$, the predator population will recover, to reach a nontrivial (u_*^1, v_*^1, r_*^1) state.*

Remark 19. The Jacobian matrix for the no cannibalism model (4) at $(0, 0, t_1/u)$ [26] is given by

$$J = \begin{bmatrix} \dfrac{t_1}{u} - 1 & 1 & 0 \\ r & -m & 0 \\ -\dfrac{t_1}{u} & 0 & -t_1 \end{bmatrix}. \tag{32}$$

Satisfaction of the following conditions,

$$u > t_1,$$
$$r < m\left(1 - \frac{t_1}{u}\right), \tag{33}$$

are sufficient to satisfy the Ruth-Hurwitz criteria for local asymptotic stability of $(0, 0, t_1/u)$. Thus if there exist cannibalism rates γ, s such that (u_*^1, v_*^1, r_*^1), the nontrivial equilibrium of the model with cannibalism (3), is globally stable and (33) also holds, then the populations will rebound from
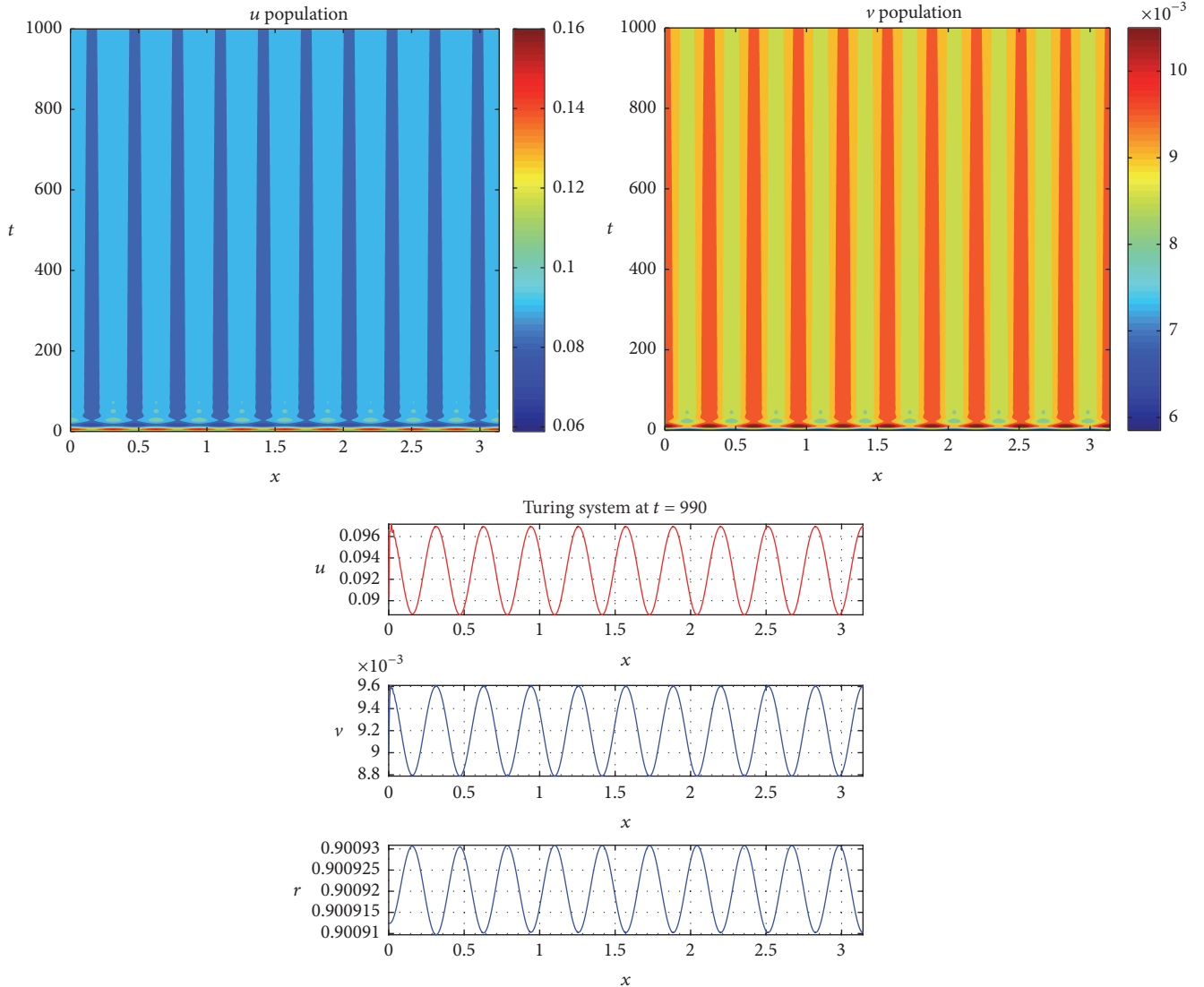
FIGURE 1: Here we demonstrate that cannibalism can indeed induce Turing instability in (8)–(10). We see a spatial Turing pattern in the juvenile species in the left panel. The right panel shows the spatial profile of all three species, after the simulation is run much longer ($t = 1000$). We see Turing persists in both the adult and juvenile predators, but the prey has very weak Turing. The values of the parameters here are $d_1 = 10^{-11}$, $d_2 = 1.7 \times 10^{-8}$, $d_3 = 0.9$, $r = 0.01$, $m = 0.1$, $\gamma = 0.01$, $s = 0.01$, $u = 0.13$, $t_1 = 0.21$. For this parameter set we see that $u_*^1 = 0.058844$, $v_*^1 = 0.005850$, $r_*^1 = 1.162736$.

$(\epsilon, \epsilon, t_1/u + \epsilon)$ and be driven up to (u_*^1, v_*^1, r_*^1). This tells us that a small amount of adult and predator populations without cannibalism *cannot* sustain themselves under certain parametric restrictions, as $(0, 0, t/u)$ is locally stable. Thus $(\epsilon, \epsilon, t/u + \epsilon)$ will be pulled back to $(0, 0, t/u)$. However, the act of cannibalism, under these parametric restrictions (assuming one can formally prove global stability of the equilibrium), can cause these small amounts of adult and juvenile predator populations to rise, and so $(\epsilon, \epsilon, t/u + \epsilon)$ can be driven up to (u_*^1, v_*^1, r_*^1).

6. Discussion and Conclusion

In the current manuscript, to the best of our knowledge, we report the *first* cannibalism induced Turing instability result,

in spatially explicit three-species age structured predator-prey systems. That is, if one considers the spatially explicit version of the three-species age structured ODE model originally proposed in [18], that is, (5), then without cannibalism there can be no Turing instability in *any* parameter regime. This is shown via Theorem 4. However, *introducing* cannibalism brings about Turing instability, in (8)–(10), seen via Theorem 14. Also note that although the Hopf bifurcation analysis on the model originally proposed by Magnússon has been done in [26], the results therein are incorrect. We derive the correct conditions for the Hopf bifurcation via Theorem 15. In the case of the prey species, we see numerical evidence of a life boat via Figure 1.

From an ecological point of view, Theorem 14 tells us that, for this *specific* model, cannibalism induces Turing instability.
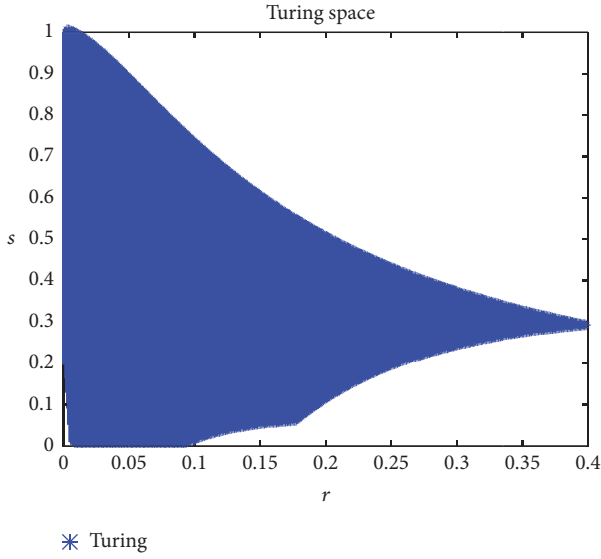
FIGURE 2: The values of the parameters here are $d_1 = 10^{-11}$, $d_2 = 1.7 \times 10^{-8}$, $d_3 = 0.9$, $\gamma = 0.01$, $m = 0.1$, $u = 0.13$, $t_1 = 0.21$. We look at the Turing space (sensitivity) generated by varying s and r, each in the range $[0, 1]$.

Thus in order to investigate the Turing instability result further, we perform a sensitivity analysis, where we look at the Turing space generated by the cannibalism parameter, with *every* other parameter in the system.

We look at how the Turing space changes as we vary s the cannibalism parameter and γ the rate of intake by the cannibalistic adult. We see that Turing occurs *everywhere* in $s \in [0, 1]$, $\gamma \in [0, 1]$, so we do not show a plot of this case. This tells us that the interplay between the amount of cannibalism and intake rate of the cannibal *always* produces Turing instability, in this range (to keep things realistic we vary the parameters only in $[0, 1]$). That is, if we keep s fixed and increase or decrease γ, the Turing instability persists.

In Figure 2 we look at how the Turing space changes with respect to the interactions between the cannibalistic adult predator and the juvenile predator. Here we vary s the cannibalism parameter and r the growth rate of the cannibalistic adult that adds to the juvenile population. We see that Turing occurs for all $s \in [0, 1]$, if r is very low, say $r \in (0, 0.03)$. For low values of s, say $s \in (0, 0.2]$, Turing occurs if we increase r up to about 0.2, but not if we further increase r. Furthermore, we observe that we lose Turing, for moderate values of r, say about 0.2 or more, if we increase s past 0.5. This tells us that the interplay between the amount of cannibalism and growth rate of the cannibalistic adult essentially always acts to remove Turing for values of $s > 0.5$. However Turing essentially persists for all s, if say $r \in (0, 0.03]$ that is very low. Now we vary s the cannibalism parameter and m the loss in the juvenile population, due to natural death as well as transitioning into the adult class. We see that Turing occurs almost everywhere except for very low values of s, m, that is, $s \in (0, 0.3]$ and $m \in (0, 0.1]$. This tells us that the interplay between the amount of cannibalism and loss rate
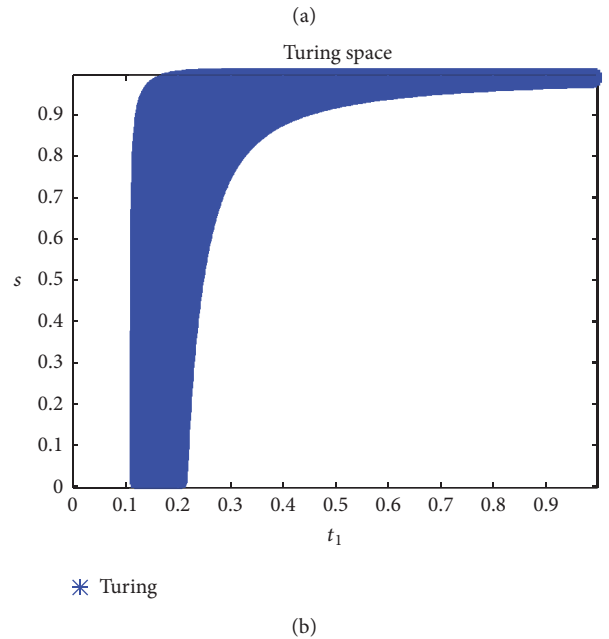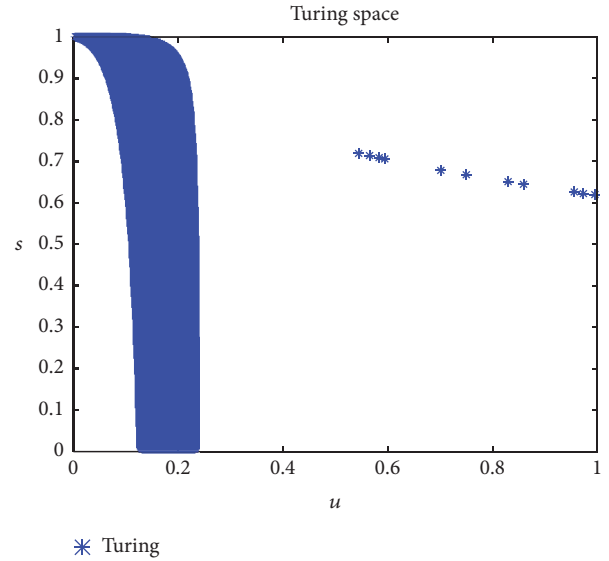

(a)

(b)

FIGURE 3: The values of the parameters in (a) are $d_1 = 10^{-11}$, $d_2 = 1.7 \times 10^{-8}$, $d_3 = 0.9$, $\gamma = 0.01$, $m = 0.1$, $r = 0.01$, $u = 0.13$. We look at the Turing space (sensitivity) generated by varying s and u, each in the range $[0, 1]$. The values of the parameters in (b) are $d_1 = 10^{-11}$, $d_2 = 1.7 \times 10^{-8}$, $d_3 = 0.9$, $\gamma = 0.01$, $r = 0.1$, $u = 0.13$, $m = 0.1$. We look at the Turing space (sensitivity) generated by varying s and t_1, each in the range $[0, 1]$.

of the juvenile essentially always acts to give Turing for most values in the considered range, so again we do not plot this case.

In Figure 3 we look at how the Turing space changes with respect to the interactions between the cannibalistic adult predator and the prey species. In Figure 3(a) we vary s the cannibalism parameter and u the growth rate of the prey. This particular interaction is probably the most interesting in our opinion. As a first analysis we noticed that Turing

occurs for all $s \in [0, 1]$, for a narrow band of u values, say $u \in [0.15, 0.22]$. However, upon further discretization of the parameter space, we observed that there are disconnected patches where Turing occurs, for roughly $s \in [0.65, 0.75]$ and $u \in [0.55, 0.6]$, and then again for certain values of $u \in [0.7, 1]$. This property is not seen in any of the other simulations, despite various further discretization in all of the parameters. In Figure 3(b) we vary s the cannibalism parameter and t_1 the competition coefficient for the prey. Note the competition mediated effects of cannibalism have been the focus of a number of recent studies [8, 36]. We see that Turing occurs for all $s \in [0, 1]$, for a narrow band of t_1 values, say $t_1 \in [0.11, 0.2]$. Also Turing occurs for essentially all t_1 values, say $t_1 \geq 0.1$, for a narrow band of s values, $s \in [0.95, 1]$. This tells us that the interplay between the amount of cannibalism and competition amongst prey essentially acts to give Turing for restricted values of competition parameter t_1.

In the same vein as the above, we also conduct a dispersion relation analysis. Here we plot the coefficient $A_1 A_2 - A_3$ for various values of the wave number k. Recall that Turing instability occurs, if this coefficient dips below the k axis. We construct a sequence of 4 graphs, by varying the cannibalism parameter s. What we notice is that as s is increased (for other parametric values fixed as in Figure 1), we see the coefficient moves upwards and then becomes positive past $s = 0.31$. This tells us that the effect of increasing cannibalism here is to remove the Turing instability.

In light of our results we can summarise a few important findings.

(1) In the spatially explicit form of the classical model considered by Magnússon and then rescaled by Tang, cannibalism *can* cause Turing instability.

(2) The Turing instability induced by cannibalism seems to be most sensitive to the prey growth rate parameter u and t_1 the competition coefficient for the prey. It also seems to be least sensitive to γ the rate of intake by the cannibalistic adult and m the loss rate in the juvenile population. This tells us that the adult predator-prey relation is critical, despite the adult being able to cannibalise the juvenile predator.

(3) Magnússon and Tang's findings are that, in the ODE model, increasing the cannibalism parameter s destabilises the system. Given that we choose similar parameters, our result suggests that, in the spatially explicit case, increasing the cannibalism parameter s removes the Turing instability and hence *stabilises* the system; see Figure 4. This makes the ODE and PDE models quite *different* dynamically.

Note the Turing patterns we currently obtain are purely spatial. It would be interesting to investigate if spatiotemporal patterns driven by Turing-Hopf type instabilities exist. If one can prove otherwise, it raises further interesting questions into the nature of cannibalism and its ecological consequences, such as why would conspecific consumption hinder temporal changes in the population, at fixed locations in space? The other interesting question for possible future
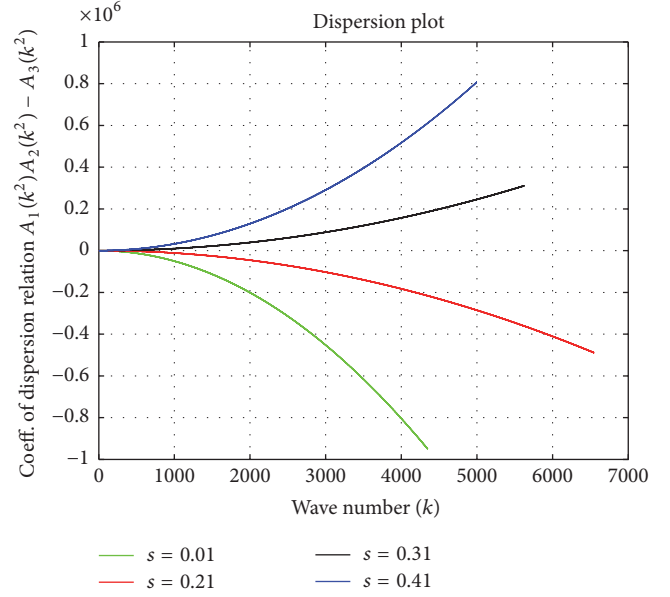

FIGURE 4: Here we plot the dispersion relation of the coefficient $A_1 A_2 - A_3$ versus the wave numbers k, for various values of the parameter s. Recall there is Turing instability when at least some part of the coefficient $A_1 A_2 - A_3$ lies below the k axis.
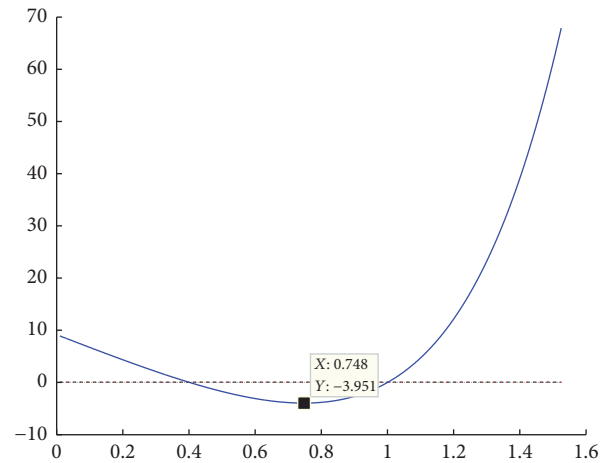

FIGURE 5: Here we see a plot of $\Phi(s)$ versus s for the other parameters as mentioned earlier from [26], $r = 0.5, m = 1, u = 0.1, \gamma = 1.5, t_1 = 1.3$. We clearly see that $(d\Phi(s)/ds)|_{s=1.001} > 0$, and $(d\Phi(s)/ds)|_{s=0.75} = 0$. The root occurs at approximately $s = 1.001$.

investigation is considering cannibalism among juveniles. We know for a fact that this does take place in certain amphibian species [36]. One might also consider the effect of cannibalism occurring simultaneously amongst adults and juveniles. Lastly, akin to [17] one can investigate the occurrence of cannibalism in the prey. Further investigation of the disconnected Turing space seen in Figure 3 should also be a future direction. The issue of whether cannibalism acts as a life boat mechanism for the predator, in (3), remains
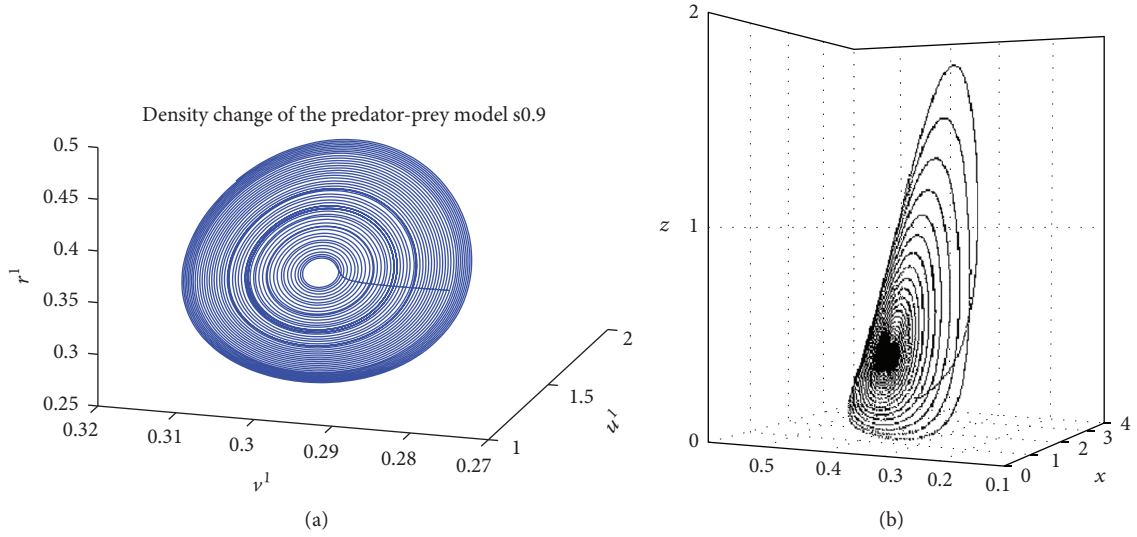
(a)

(b)

FIGURE 6: Here we take the parameters as mentioned earlier from [26], $r = 0.5, m = 1, u = 0.1, \gamma = 1.5, t_1 = 1.3, s = 0.9$. We clearly see that, at $s = 0.9$, $\Phi < 0$, from Figure 5, and we expect limit cycle dynamics, which we see in (a). We compare to the simulation from [26] in (b), which shows a stable spiral at $s = 0.9$, which is clearly incorrect.
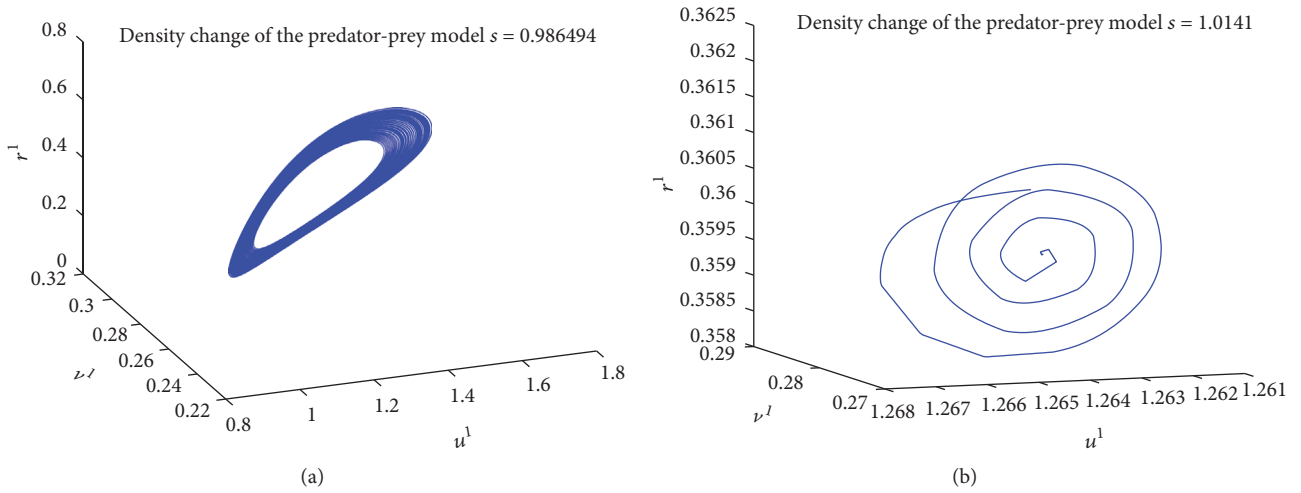

(a)

(b)

FIGURE 7: Here we take the parameters as mentioned earlier from [26], $r = 0.5, m = 1, u = 0.1, \gamma = 1.5, t_1 = 1.3$. With $s = 0.986494$, $\Phi < 0$, from Figure 5, and we clearly see limit cycle dynamics, as expected in (a). Now if we take $s = 1.0141$, where $\Phi > 0$, from Figure 5, we see a stable spiral, again as expected, in (b).

unproven and can also be considered in future. All in all, we hope that the current work leads to further investigations and collaborations into the fascinating effects of cannibalism and the often *counterintuitive* role it plays in natural predator-prey communities.

Appendix

A. Equilibrium and Stability Analysis of Model with Cannibalism

The interior equilibrium point for (3) is given by

$$
u_*^1 = \frac{-(m - st_1 + su - rsu\gamma) \pm \sqrt{(m - st_1 + su - rsu\gamma)^2 - 4(-ru - mt_1 + mu)}}{2},
$$

$$
v_*^1 = \frac{ru_*^1}{(m + su_*^1)},
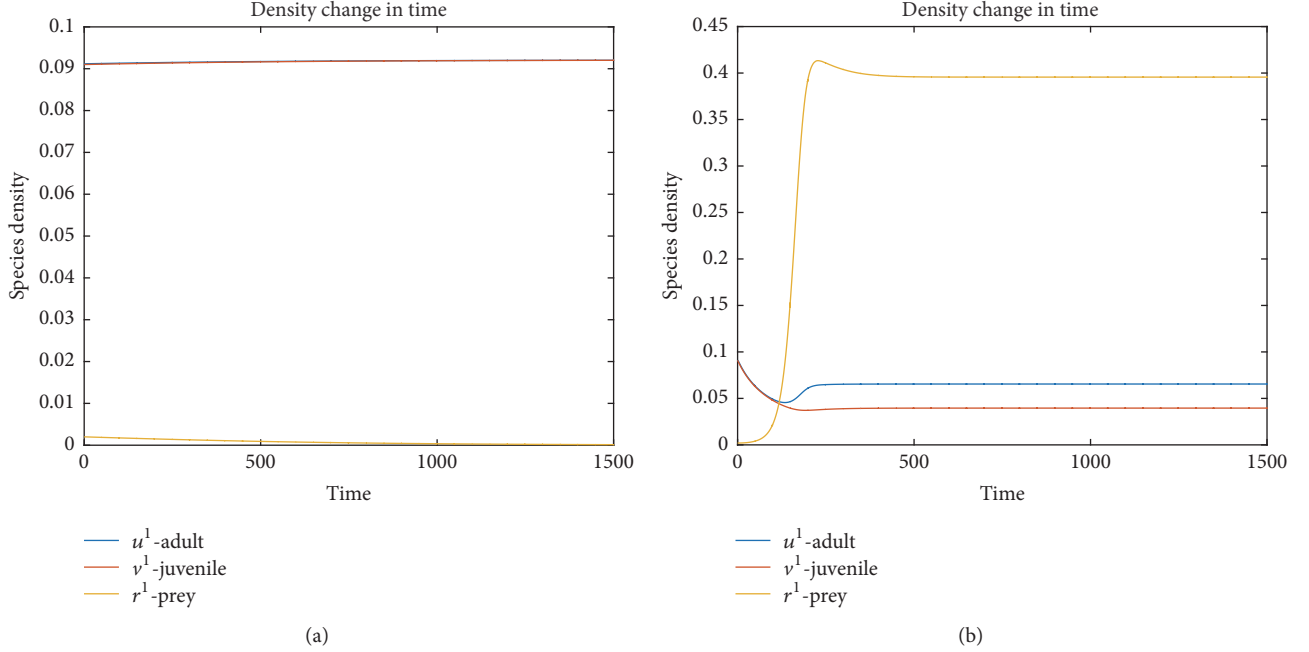$$

$$
r_*^1 = \frac{t_1 - u_*^1}{u}.
$$

(A.1)

(a)

(b)

FIGURE 8: Here we demonstrate that cannibalism can act as a lifeboat for the prey species also. The values of the parameters here are $r = 0.01$, $m = 0.01$. $\gamma = 0.01$, $u = 0.062$, $t_1 = 0.09$. We see in (a) that, with $s = 0$, or no cannibalism, the prey is driven to extinction. However, in (b), we see that introducing a little bit of cannibalism, that is, by choosing $s = 0.1$, the prey population immediately rebounds to a high level.

The Jacobian matrix of system (3) evaluated at the interior equilibrium (u_*^1, v_*^1, r_*^1) is given by

$$J = \begin{bmatrix} r_*^1 - 1 + \gamma s v_*^1 & 1 + \gamma s u_*^1 & u_*^1 \\ r - s v_*^1 & -m - s u_*^1 & 0 \\ -r_*^1 & 0 & t_1 - 2u r_*^1 - u_*^1 \end{bmatrix}. \quad \text{(A.2)}$$

B. Derivation of Characteristic Polynomial

Here we focus on working out the coefficients of the characteristic polynomial $\det(J - \lambda I)$, where J is as in (A.2). These coefficients are critical in order to correctly work out Hopf bifurcations that occur in (3). The characteristic equation is standard,

$$\lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 = 0, \quad \text{(B.1)}$$

where

(1) $A_1 = -(J_{11} + J_{22} + J_{33})$;

(2) $A_3 = -(J_{11}J_{22}J_{33}) + (J_{11}J_{32}J_{23}) + (J_{21}J_{12}J_{33}) - (J_{12}J_{31}J_{23}) - (J_{13}J_{21}J_{32}) + (J_{13}J_{31}J_{22})$;

(3) $A_2 = (J_{11}J_{33}) + (J_{11}J_{22}) + (J_{22}J_{33}) - (J_{23}J_{32}) - (J_{21}J_{12}) - (J_{13}J_{31})$.

Straightforward computations show that $A_1 > 0$ and $A_3 > 0$ if and only if the following conditions are satisfied:

(i) $A_1 = -(J_{11} + J_{22} + J_{33}) > 0, \Rightarrow -(r_*^1 + \gamma s v_*^1 - 1 - m - s u_*^1 + (u_*^1 - t_1)) > 0 \Rightarrow -r_*^1 - \gamma s v_*^1 + 1 + m + s u_*^1 - u_*^1 + t_1 > 0 \Rightarrow 1 + m + t_1 - r_*^1 - u_*^1 > s(\gamma v_*^1 - u_*^1)$.

Thus if $(\gamma v_*^1 - u_*^1) > 0$, then $A_1 > 0$, if

$$\frac{1 + m + t_1 - r_*^1 - u_*^1}{(\gamma v_*^1 - u_*^1)} > s. \quad \text{(B.2)}$$

However if $(\gamma v_*^1 - u_*^1) < 0$, then $A_1 > 0$, if

$$\frac{1 + m + t_1 - r_*^1 - u_*^1}{(\gamma v_*^1 - u_*^1)} < s. \quad \text{(B.3)}$$

(ii) $A_3 = -(J_{11}J_{22}J_{33}) + (J_{11}J_{32}J_{23}) + (J_{21}J_{12}J_{33}) - (J_{12}J_{31}J_{23}) - (J_{13}J_{21}J_{32}) + (J_{13}J_{31}J_{22}) > 0$,

$$A_3 = \left[\left(r_*^1 - 1 + \gamma s v_*^1\right)\left(m + s u_*^1\right)\left(u_*^1 - t_1\right)\right]$$

$$+ \left[\left(r - s v_*^1\right)\left(1 + \gamma s u_*^1\right)\left(u_*^1 - t_1\right)\right]$$

$$+ \left[u_*^1 r_*^1 \left(m + s u_*^1\right)\right] > 0. \quad \text{(B.4)}$$

Thus $[(u_*^1)^2 - 2(u_*^1)^2 r_*^1 - t_1 u_*^1 + u_*^1 v_*^1 - r\gamma(u_*^1)^2 + t_1 u_*^1 r_*^1 + m\gamma t_1 v_*^1 + r\gamma t_1 u_*^1 - m\gamma u_*^1 v_*^1 - t_1] > 0$.

Then $A_3 > 0$ if

$$\frac{\left[mt_1 - mu_*^1 - rt_1 + ru_*^1 - mt_1 r_*^1 v_*^1 + 2mu_*^1 r_*^1\right]}{\left[(u_*^1)^2 - 2(u_*^1)^2 r_*^1 - t_1 u_*^1 + u_*^1 v_*^1 - r\gamma(u_*^1)^2 + t_1 u_*^1 r_*^1 + m\gamma t_1 v_*^1 + r\gamma t_1 u_*^1 - m\gamma u_*^1 v_*^1 - t_1\right]} > s. \tag{B.5}$$

(iii) $A_2 = (J_{11}J_{33}) + (J_{11}J_{22}) + (J_{22}J_{33}) - (J_{23}J_{32}) - (J_{21}J_{12}) - (J_{13}J_{31})$.

$$A_2 = \left((r_*^1 - 1 + \gamma s v_*^1)(u_*^1 - T_1)\right)$$
$$+ \left((r_*^1 - 1 + \gamma s v_*^1)(-m - s u_*^1)\right)$$
$$+ \left((-m - s u_*^1)(u_*^1 - t_1)\right) \tag{B.6}$$
$$- \left((1 + \gamma s u_*^1)(r - s v_*^1)\right) + (u_*^1 r_*^1).$$

Thus $A_2 > 0$ if the following holds true.

$$m - r + t_1 - u_*^1 + mt_1 - mu_*^1 - mr_*^1 + su_*^1 + sv_*^1$$
$$- t_1 r_*^1 + 2u_*^1 r_*^1 - s(u_*^1)^2 + st_1 u_*^1 - su_*^1 r_*^1 \tag{B.7}$$
$$- ms\gamma v_*^1 - rs\gamma u_*^1 - s\gamma t_1 v_*^1 + s\gamma u_*^1 v_*^1 > 0.$$

We now check when $A_1 A_2 - A_3 > 0$.

$$A_1 A_2 - A_3 = rt_1 - mt_1 + mu_*^1 - ru_*^1 + s(u_*^1)^2$$
$$- 2s(u_*^1)^2 r_*^1 + mt_1 r_*^1 - st_1 u_*^1$$
$$- st_1 v_*^1 - 2mu_*^1 r_*^1 + su_*^1 v_*^1 \tag{B.8}$$
$$- rs\gamma(u_*^1)^2 + st_1 u_*^1 r_*^1 + ms\gamma t_1 v_*^1$$
$$+ rs\gamma t_1 u_*^1 - ms\gamma u_*^1 v_*^1 > 0.$$

We set

(i) $A_1(s)A_2(s) - A_3(s) = as^2 + bs + c = 0$, where

(ii) $c = m - r + t_1 - u_*^1 + t_1(r_*^1)^2 - t_1^2 r_*^1 - 2u_*^1(r_*^1)^2 - 2(u_*^1)^2 r_*^1 + 2mt_1 + t_1^2 - 2mu_*^1 - 2mr_*^1 + rr_*^1 + (u_*^1)^2 - 2t_1 u_*^1 - 2t_1 r_*^1 + mt_1^2 + m^2 t_1 + 3u_*^1 r_*^1 + m(u_*^1)^2 - m^2 u_*^1 + m(r_*^1)^2 - m^2 r_*^1 - mr + m^2 + 3t_1 u_*^1 r_*^1 - 2mt_1 u_*^1 - 2mt_1 r_*^1 + 2mu_*^1 r_*^1$,

(iii) $b = u_*^1 + v_*^1 - 2t_1(u_*^1)^2 + t_1^2 u_*^1 + u_*^1(r_*^1)^2 + 2(u_*^1)^2 r_*^1 + 2mu_*^1 + mv_*^1 - ru_*^1 - 2(u_*^1)^2 + (u_*^1)^3 + 2t_1 u_*^1 - 2u_*^1 r_*^1 - v_*^1 r_*^1 - 2m(u_*^1)^2 - m^2\gamma v_*^1 - 2t_1 u_*^1 r_*^1 - \gamma t_1^2 v_*^1 - \gamma(u_*^1)^2 v_*^1 - 2m\gamma v_*^1 - r\gamma u_*^1 + r\gamma v_*^1 - 2mu_*^1 r_*^1 - 2\gamma t_1 v_*^1 + 2\gamma u_*^1 v_*^1 + 2\gamma t_1 u_*^1 v_*^1 + 2\gamma t_1 v_*^1 r_*^1 - 3\gamma u_*^1 v_*^1 r_*^1 - mr\gamma u_*^1 + 2mst_1 u_*^1 - 2m\gamma t_1 v_*^1 + 2m\gamma u_*^1 v_*^1 + 2m\gamma v_*^1 r_*^1 + r\gamma u_*^1 r_*^1$,

(iv) $a = -(u_*^1 - \gamma v_*^1)((u_*^1)^2 - v_*^1 - u_*^1 - t_1 u_*^1 + u_*^1 r_*^1 + m\gamma v_*^1 + r\gamma u_*^1 + \gamma t_1 v_*^1 - \gamma u_*^1 v_*^1)$.

Thus $A_1 A_2 - A_3 > 0$ if

$$b^2 - 4ac < 0, \quad a > 0, \tag{B.9}$$

where a, b, c are given above.

C. General Criteria for Turing Instability

We first recap certain general criteria regarding Turing instability in three-species models following [19]. Let us consider a general three-species reaction diffusion system:

$$u_t = d_1 u_{xx} + f(u, v, r)$$
$$v_t = d_2 v_{xx} + g(u, v, r) \tag{C.1}$$
$$r_t = d_3 r_{xx} + h(u, v, r).$$

We prescribe Neumann boundary conditions,

$$u_x = v_x = r_x = 0, \tag{C.2}$$

and suitable positive initial conditions,

$$u(x, 0) > 0,$$
$$v(x, 0) > 0, \tag{C.3}$$
$$r(x, 0) > 0.$$

Consider the linearization of (C.1) about the positive interior equilibrium point (u^*, v^*, r^*), which is the spatially homogenous solution to (C.1).

Consider a small space time perturbation, that is,

$$\mathbf{W} = U - U^* = O(\epsilon), \quad \text{where } \epsilon \longrightarrow 0, \tag{C.4}$$

with $U^* = (u^*, v^*, r^*)$. Substituting and collecting linear terms of order $O(\mathbf{W})$, we obtain

$$\frac{\partial \mathbf{W}}{\partial t} = \mathbf{D}\Delta\mathbf{W} + \mathbf{J}\mathbf{W}, \tag{C.5}$$

$$\Delta\mathbf{W}_i \cdot \mathbf{n} = 0 \quad \text{for } x \in \partial\Omega, \ i = 1, 2, 3, \tag{C.6}$$

where

$$\mathbf{D} = \begin{bmatrix} d_1 & 0 & 0 \\ 0 & d_2 & 0 \\ 0 & 0 & d_3 \end{bmatrix} \tag{C.7}$$

is the diffusion matrix and

$$\mathbf{J} = \begin{bmatrix} J_{11} & J_{12} & J_{13} \\ J_{21} & J_{22} & J_{23} \\ J_{31} & J_{32} & J_{33} \end{bmatrix} \tag{C.8}$$

is the Jacobian matrix associated with the reaction terms of (C.1).

Let

$$\mathbf{W}\left(\varepsilon, t\right) = \begin{bmatrix} \overline{u}_0 \\ \overline{u}_1 \\ \overline{u}_2 \end{bmatrix} e^{\lambda t + ik\varepsilon}, \tag{C.9}$$

where ε is the spatial coordinate in Ω, $\overline{u}_i$ $(i = 0, 1, 2)$ is the amplitude, λ is the eigenvalues associated with the interior equilibrium point, (u_*^1, v_*^1, r_*^1), and k is the wave number of the solution. Upon substituting, we obtain the characteristic equation

$$\left| \mathbf{J} - \lambda \mathbf{I} - k^2 \mathbf{D} \right| = 0, \tag{C.10}$$

where $\mathbf{I}$ is a 3×3 identity matrix. The sign of $\text{Re}(\lambda)$ indicates the stability, or lack thereof, of the equilibrium point (u^*, v^*, r^*). The dispersion relation is

$$P\left(\lambda\right) = A_3\left(k^2\right)\lambda^3 + A_2\left(k^2\right)\lambda^2 + A_1\left(k^2\right)\lambda$$
$$+ A_0\left(k^2\right), \tag{C.11}$$

where

$$A_1\left(k^2\right) = -\left(J_{11} + J_{22} + J_{33}\right) + \left(d_1 + d_2 + d_3\right)k^2 \tag{C.12}$$

$$A_2\left(k^2\right) = \left[\left(J_{11}J_{33}\right) + \left(J_{11}J_{22}\right) + \left(J_{22}J_{33}\right) - \left(J_{23}J_{32}\right)\right.$$
$$\left. - \left(J_{21}J_{12}\right) - \left(J_{13}J_{31}\right)\right] + k^2\left[d_3 J_{22} + d_2 J_{33} + d_1 J_{33}\right.$$
$$\left. + d_1 J_{22} + d_2 J_{11} + d_3 J_{11}\right] + \left(k^2\right)^2\left[d_2 d_3 + d_2 d_1\right.$$
$$\left. + d_1 d_3\right] \tag{C.13}$$

$$A_3\left(k^2\right) = \left[-\left(J_{11}J_{22}J_{33}\right) + \left(J_{11}J_{32}J_{23}\right) + \left(J_{21}J_{12}J_{33}\right)\right.$$
$$\left. - \left(J_{12}J_{31}J_{23}\right) - \left(J_{13}J_{21}J_{32}\right) + \left(J_{13}J_{31}J_{22}\right)\right]$$
$$+ k^2\left[-d_3 J_{12}J_{21} - d_2 J_{31}J_{13} - d_1 J_{32}J_{23} + d_1 J_{22}J_{33}\right.$$
$$\left. + d_2 J_{11}J_{33} + d_3 J_{11}J_{22}\right] + \left(k^2\right)^2\left[d_1 d_2 J_{33}\right. \tag{C.14}$$
$$\left. + d_1 d_3 J_{22} + d_3 d_2 J_{11}\right] + \left(k^2\right)^3\left[d_1 d_2 d_3\right].$$

Now $\text{Re}(\lambda) < 0$ provided that
$A_n(k^2) > 0$, for $n = 0, 1, 2, 3$, and $A_1(k^2)A_2(k^2) - A_3(k^2) > 0$.

Diffusion-driven instability requires that the stable, homogeneous steady state is driven unstable by the interaction of the dynamics and diffusion of the species, and, therefore, from the arguments given above we are interested in obtaining conditions such that $\text{Re}(\lambda(k^2 = 0)) < 0$ and $\text{Re}(\lambda(k^2 > 0)) > 0$, for some $k^2 > 0$. Note $A_1(k^2) = \alpha + \beta(k^2)$, where $\alpha = -(J_{11} + J_{22} + J_{33})$, $\beta = (d_1 + d_2 + d_3)$, and $A_1(k^2) > 0$ if $\alpha > 0$.

Note that $A_3(k^2)$ and $A_1(k^2)A_2(k^2) - A_3(k^2)$ are both cubic functions of (k^2) of the form $b(k^2)^3 + c(k^2)^2 + d(k^2) + h$ with $b \geq 0$ and $h > 0$. If it exists, the minimum turning point

for $y(k^2) = b(k^2)^3 + c(k^2)^2 + d(k^2) + h$ (which is calculated from $dy/dk^2 = 0$ and $d^2 y/d(k^2)^2 > 0$) occurs at

$$k^2 = k_{TP}^2 = \frac{-c + \left[\sqrt{c^2 - 3bd}\right]}{3b}. \tag{C.15}$$

Now k_{TP}^2 is real and positive if $d < 0$ or $c < 0$ (and $c^2 > 3bd$). The coefficients b, c, d, h of $A_3(k^2)$ and $A_1(k^2)A_2(k^2) - A_3(k^2)$ are worked out in detail in Table 1.

We refer the reader to a detailed analysis of this in [19]. However, we can summarise the necessary conditions for Turing instability from [19] via the following theorem.

Theorem C.1. *Consider the three-species reaction diffusion system (5). For the spatially homogenous steady state (u^*, v^*, r^*) to be driven unstable due to diffusion, it is necessary that the coefficients c, d of A_3, as well as the coefficients c, d of $A_1 A_2 - A_3$, from Table 1 be strictly negative and $c^2 - 3bd$ be strictly positive.*
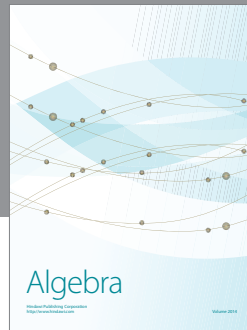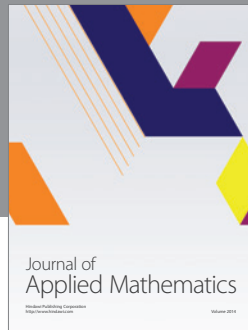
Competing Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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