

## Models for the effect of toxicant in single-species and predator-prey systems

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**Abstract.** Models of single-species and predator-prey systems in a polluted closed environment are developed and partially analyzed. Three cases are considered: a single influx of toxicant, a constant influx of toxicant, and a periodic pollution of the environment. In the case of single-species growth we are able to determine some local and global dynamics. In the case of predator-prey systems, we investigate the existence of steady states for a small constant influx of toxicant.

**Key words:** Single-species – Predator-prey – Toxicants – Equilibria – Stability – Periodic perturbation

### 1 Introduction

The question of the effects of pollutants and toxicants on ecological communities is of great interest from both environmental and conservational points of view. Some examples are oil pollution in the seas, Nelson (1970), degradation of forests, Shukla et al. (1989), Woodman and Cowling (1987), and dumping of toxic waste in rivers and lakes, Haas (1981), Jensen and Marshall (1982).

In a series of papers (de Luna and Hallam (1987); Hallam and Clark (1982); Hallam, Clark and Jordan (1983); Hallam, Clark and Lassiter (1983); Hallam and de Luna (1984)), T. G. Hallam and his coworkers studied the effects of toxicants on various ecosystems by utilizing mathematical models. In particular Hallam et al. (1983) have modelled the interaction of toxicant in the environment with the population by assuming that the growth rate of population density linearly depends upon the toxicant concentration in the population but they do not consider the effect of environmental toxicant on the carrying capacity. In their models the differential equation governing the concentration of toxicant in the population does not explicitly depend upon the density of the population as

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this concentration has been defined with respect to the biomass of the total population and not with respect to total mass or volume of the environment where the population lives. The equation governing the concentration of the toxicant in the environment which has been defined with respect to the mass of the environment does however involve the population density as well as the toxicant concentration in the population. We feel that if all the concentrations i.e., biomass of the population, toxicant in the population and toxicant in the environment, are defined with respect to mass or volume of the total environment in which the population lives, the model of the ecotoxicological problem becomes more visible as each of the equations will then in general involve all these variables.

In this paper we therefore consider single-species and predator-prey interactions in a closed homogeneous environment the carrying capacity of which is also affected by the exogenous introduction of toxicant. We model the interactions of the populations and the toxicants in the population and in the environment by means of ordinary differential equations in terms of their concentrations defined with respect to mass or volume of the total environment where the population lives.

We are interested in determining as much as possible, the effects of the toxicant on equilibrium levels, and stability of the biological systems.

In the next section we develop the single-species model and carry out the analysis for three cases, namely an instantaneous introduction of toxicant (e.g. a one-time dumping of pollutant in a lake), a constant introduction of toxicant into the environment (e.g. chimney exhaust into the atmosphere affecting a forest), and a small amplitude fluctuating introduction of toxicant (e.g. oil pollution along a shoreline due to wave action after a spill).

In Sect. 3, we consider the first two cases as affecting a predator-prey system. Here, the question of the existence of a nontrivial equilibrium is itself nontrivial. In the final section we discuss our results and suggest future work.

The population models are based on those described in Freedman (1987). We assume that all functions utilized are sufficiently smooth that solutions to initial value problems exist uniquely and are continuable for all positive time.

## 2 Single-species

We utilize a modified logistic equation (Freedman, 1987) to model the effect of toxin on single-species growth. We let

$$\begin{aligned} x(t) &= \text{Concentration of the population biomass} \\ &= \frac{\text{mass (or volume) of the population biomass}}{\text{mass (or volume) of the total environment where the population lives}} \end{aligned}$$

$$\begin{aligned} T(t) &= \text{Concentration of toxicant in the environment} \\ &= \frac{\text{mass (or volume) of the toxicant in the environment}}{\text{mass (or volume) of the total environment}} \end{aligned}$$

$$\begin{aligned} U(t) &= \text{Concentration of toxicant in the population} \\ &= \frac{\text{mass (or volume) of the toxicant in the total population}}{\text{mass (or volume) of the total environment}} \end{aligned}$$

We think of population change as made up of birth minus death.

We assume that the population is affected by the toxicant as follows: growth of  $x$  is diminished by the presence of toxicant  $U$  in  $x$ , whereas the carrying capacity of the environment is lowered by the presence of toxicant  $T$  in the environment. Here  $U$  and  $x$  represent different concentrations.

It is assumed that the toxicant in the environment is washed out or broken down with rate  $\delta_0$ . Such can occur if the environment is a lake which upon occasion drains into another body of water, or if the toxicant is subject to chemical decomposition. Further, it is assumed that toxicant from the environment is absorbed by the population in direct proportion to their concentration (i.e.  $\alpha_1 x T$ ). The toxicant in the population may also be removed from the total environment directly with rate  $\delta_1$ . Toxicant may also be removed from the population in proportion to their concentrations, some of it ( $\pi_1 \gamma_1 x T$ ) reentering the environment, and some removed from the environment. Finally, toxicant may be externally introduced into the environment according to some prescribed rate  $f(t)$ .

This leads to the following system of ordinary differential equations

$$\begin{aligned}\dot{x} &= r(U)x - \frac{r_0 x^2}{K(T)} \\ \dot{T} &= -\delta_0 T - \alpha_1 x T + \pi_1 \gamma_1 x U + f(t) \\ \dot{U} &= -\delta_1 U + \alpha_1 x T - \gamma_1 x U, \\ x(0) &\geq 0, \quad T(0) \geq 0, \quad U(0) \geq kx(0),\end{aligned}\tag{2.1}$$

where  $\delta_0, \delta_1, \alpha_1, \gamma_1, k$  are positive constants, and  $0 \leq \pi_1 \leq 1$ , and where  $\delta_0$  is the depletion rate of toxicant in the environment,

$\delta_1$  is the depletion rate of the toxicant in the population,

$\alpha_1$  in the second equation of (2.1) is the depletion rate of toxicant in the environment due to its intake by the population,

$\gamma_1$  in the third equation of (2.1) is the depletion rate of toxicant in the population due to their death (removal).

In the model (2.1) we have assumed that the initial toxicant  $U(0)$  depends upon the initial population  $kx(0)$ . To explain why this is reasonable consider the following particular cases

(I)  $x(0) = 0, \quad \alpha_1 \neq 0$

(II)  $x(0) \neq 0, \quad \alpha_1 = 0$  (negligible intake of toxicant by the population).

*Case I* In this case from the first equation of (2.1) we have  $x(t) \equiv 0$ . We then get from the third equation of (2.1)

$$\dot{U} = -\delta_1 U$$

or

$$U = U(0) e^{-\delta_1 t}.$$

Since  $x(t) \equiv 0$ , from physical considerations we must have  $U(t) \equiv 0$  [by definition of  $U(t)$ ]. This suggests that  $U(0)$  must be zero implying that  $U(0) = kx(0)$  is meaningful. (Note  $x(0) = 0$ .)

*Case II* In this case from the first equation of (2.1) we have  $x(t) \leq K(0)$ . Then

from the third equation we can obtain  $U(t) \equiv 0$  if  $U(0) = 0$ . Thus in this case if  $U(0) = kx(0)$  is to be meaningful we must put  $k = 0$ .

Thus we may conclude the relation  $U(0) = kx(0) \geq 0$  is correct. Here  $k \geq 0$  may be interpreted as the proportionality constant determining the measure of initial toxicant concentration in the population at  $t = 0$ .

$r(U)x$  is the birth component of our population and hence  $r(U)$  represents the growth rate "constant" which is affected by  $U$ . Hence we assume

$$\begin{aligned} r(0) = r_0 > 0, \quad r'(U) < 0 \quad \text{for } U \geq 0, \\ r(\bar{U}) = 0 \quad \text{for some } \bar{U} > 0. \end{aligned} \quad (2.2)$$

The death component is given by  $r_0x^2/K(T)$ , where  $K(T)$  represents the carrying capacity which is affected by  $T$ . Hence we assume

$$\begin{aligned} K(0) = K_0 > 0, \quad K'(T) < 0 \quad \text{for } T \geq 0, \\ K(\bar{T}) = 0 \quad \text{for some } \bar{T} > 0. \end{aligned} \quad (2.3)$$

The above assumptions imply that increasing toxicant decreases birth rate and increases death rate, and in particular the existence of  $\bar{U}$  and  $\bar{T}$  imply that if the toxicant level is sufficiently high, then the population cannot reproduce or grow, and in fact will die ( $K(\bar{T}) = 0$ ).

$f(t)$  represents the rate of introduction of toxicant into the environment beyond the initial concentration. We analyze our model for three possible types of such  $f(t)$ , namely  $f(t)$  zero,  $f(t)$  constant, and  $f(t)$  a periodic perturbation of a constant value.

Model (2.1) presumes certain averaging effects, that is it presumes a uniform environment, an average age class, average fertility, etc. Although individuals in any population will vary and environments are inevitably patchy to some extent, such presumptions are standard in the literature and in many cases a reasonable approximation for modelling purposes (see Freedman, 1987, and the references therein).

### 2.1 $f(t) \equiv 0$

In this case our model has two nonnegative equilibria in  $x - T - U$  space when  $0 \leq T < \bar{T}$ ,  $0 \leq U < \bar{U}$ , namely  $E_0(0, 0, 0)$  and  $E_1(K_0, 0, 0)$ . To determine the local stability of these equilibria, we compute the variational matrices about these equilibria, which we denote  $M_0$  and  $M_1$ , respectively.

$$M_0 = \begin{bmatrix} r_0 & 0 & 0 \\ 0 & -\delta_0 & 0 \\ 0 & 0 & -\delta_1 \end{bmatrix},$$

$$M_1 = \begin{bmatrix} -r_0 & r_0K'(0) & r'(0)K_0 \\ 0 & -\delta_0 - \alpha_1K_0 & \pi_1\gamma_1K_0 \\ 0 & \alpha_1K_0 & -\gamma_1K_0 - \delta_1 \end{bmatrix}.$$

From the above, it is clear that  $E_0$  is a hyperbolic saddle point, locally stable in the  $T$  and  $U$  directions and locally unstable in the  $x$  direction.  $E_1$  is locally asymptotically stable. However, we can say much more in this case as given by the following theorem.

**Theorem 2.1** *If  $x(0) > 0$ , then  $E_1$  is globally asymptotically stable with respect to the nonnegative orthant.*

*Proof.* First note that

$$\dot{x}(t) = r(U)x - \frac{r_0 x^2}{K(T)} \leq r_0 \left( x - \frac{x^2}{K_0} \right).$$

Hence  $\lim_{t \rightarrow \infty} x(t) \leq K_0$ . Now consider

$$\dot{T} + \dot{U} = -\delta_0 T - \delta_1 U + (\pi_1 - 1)\gamma_1 x U \leq -\delta(T + U),$$

where  $\delta = \min(\delta_0, \delta_1)$ . Then  $T(t) + U(t) \leq (T(0) + U(0)) e^{-\delta t}$  and hence the system is dissipative.

From the above it follows that  $\lim_{t \rightarrow \infty} T(t) = \lim_{t \rightarrow \infty} U(t) = 0$ . Hence in the limit  $x(t)$  is given by solutions of  $\dot{x}(t) = r_0 x(1 - x/K_0)$ . Since  $x(0) > 0$ , the theorem follows.

This case corresponds to a single introduction (possibly instantaneous) of toxicant into the environment. Theorem 2.1 shows that provided the concentration was not sufficient to kill all the population, eventually the toxicant would be removed and the population would recover to its former level.

## 2.2 $f(t) \equiv Q > 0$

Again, provided  $0 \leq T < \bar{T}$  and  $0 \leq U < \bar{U}$ , there are two nonnegative equilibria,  $E_2(0, Q/\delta_0, 0)$  and  $\tilde{E}(\tilde{x}, \tilde{T}, \tilde{U})$ .

We now formulate criteria for  $\tilde{E}$  to exist. We require that the system of algebraic equations

$$\begin{aligned} r(\tilde{U}) - \frac{r_0 \tilde{x}}{K(\tilde{T})} &= 0 \\ \delta_0 \tilde{T} + \alpha_1 \tilde{x} \tilde{T} - \pi_1 \gamma_1 \tilde{x} \tilde{U} - Q &= 0 \\ \alpha_1 \tilde{x} \tilde{T} - \gamma_1 \tilde{x} \tilde{U} - \delta_1 \tilde{U} &= 0 \end{aligned} \tag{2.4}$$

has a positive solution. The first of these gives  $\tilde{x} = r(\tilde{U})K(\tilde{T})/r_0$ . Substituting for  $\tilde{x}$  in the other two equations gives

$$\alpha_1 \tilde{T} = \left[ \gamma_1 + \frac{\delta_1 r_0}{r(\tilde{U})K(\tilde{T})} \right] \tilde{U} \tag{2.5}$$

and

$$\delta_0 \tilde{T} = Q - [\delta_1 + (1 - \pi_1)\gamma_1 r(\tilde{U})K(\tilde{T})/r_0] \tilde{U}. \tag{2.6}$$

Here, we have

$$\tilde{T} = \frac{Q}{\delta_0} - \left[ \delta_1 + (1 - \pi_1) \frac{\gamma_1}{\nu_0} r(\tilde{U})k(\tilde{T}) \right] \frac{\tilde{U}}{\delta_0}$$

which implies

$$\tilde{T} \rightarrow \frac{Q}{\delta_0} \quad \text{when } \tilde{U} \rightarrow 0$$

and

$$\tilde{T} \rightarrow \frac{1}{\delta_0} (Q - \delta_1 \bar{U}) \quad \text{when } \tilde{U} \rightarrow \bar{U} \text{ for } \tilde{T} < \bar{T}.$$

This implies that  $Q \geq \delta_1 \bar{U}$  for  $\tilde{T} \geq 0$ . We can also obtain,

$$\begin{aligned} \frac{d\tilde{T}}{d\tilde{U}} = & -\frac{1}{\delta_0} \left[ \delta_1 + (1 - \pi_1) \frac{v_1}{r_0} r(\tilde{U}) K(\tilde{T}) \right] \\ & - \frac{\tilde{U}}{\delta_0} (1 - \pi_1) \frac{v_1}{r_0} \left\{ r'(\tilde{U}) K(\tilde{T}) + r(\tilde{U}) K'(\tilde{T}) \frac{d\tilde{T}}{d\tilde{U}} \right\}. \end{aligned}$$

When  $\tilde{U} \rightarrow 0$ ,  $d\tilde{T}/d\tilde{U}$  is negative for  $\tilde{T} < \bar{T}$ . When  $\tilde{U} \rightarrow \bar{U}$ , we get,

$$\begin{aligned} \frac{d\tilde{T}}{d\tilde{U}} = & -\frac{1}{\delta_0} \left[ \delta_1 + \bar{U} (1 - \pi_1) \frac{v_1}{r_0} K(\bar{q}) r'(\bar{U}) \right] \\ \leq & 0 \end{aligned}$$

provided

$$\delta_1 \geq \bar{U} (1 - \pi_1) \frac{v_1}{r_0} K(0) \alpha_m$$

where  $-r'(\bar{U}) \leq \alpha_m$ .

Thus, in our model we assume the following conditions in addition to (2.2) and (2.3),

- (i)  $Q \geq \delta_1 \bar{U}, \quad \tilde{T} < \bar{T}$
- (ii)  $\delta_1 \geq \bar{U} (1 - \pi_1) \frac{v_1}{r_0} K(0) \alpha_m$
- (iii)  $-r'(\bar{U}) \leq \alpha_m$ .

As far as Eq. (2.5) is concerned,  $\tilde{T}$  is an increasing function of  $\tilde{U}$  since  $d\tilde{T}/d\tilde{U} > 0$  for  $\tilde{U} < \bar{U}, \tilde{T} < \bar{T}$ . This can be checked after differentiating  $\tilde{T}$  from (2.3) with respect to  $\tilde{U}$ .

With the above assumptions, Eq. (2.5) represents  $\tilde{T}$  as an increasing from zero function of  $\tilde{U}$  and Eq. (2.6) represents  $\tilde{T}$  as a decreasing from  $Q/\delta_0$  function of  $\tilde{U}$ , which approaches or intersects zero. Hence the two graphs must intersect and provided the intersection values  $\tilde{T} < \bar{T}$  and  $\tilde{U} < \bar{U}$ , then  $\tilde{E}$  exists.

We refer to Fig. 1 for the graphs of Eqs. (2.5) and (2.6) in the nonnegative  $\tilde{U} - \tilde{T}$  plane.

The variational matrices corresponding to  $E_2$  and  $\tilde{E}$  are denoted by  $M_2$  and  $\tilde{M}$ , respectively and are computed as follows.

$$\begin{aligned} M_2 = & \begin{bmatrix} r_0 & 0 & 0 \\ -\alpha_1 Q/\delta_0 & -\delta_0 & 0 \\ \alpha_1 Q/\delta_0 & 0 & -\delta_1 \end{bmatrix}, \\ \tilde{M} = & \begin{bmatrix} -r(\tilde{U}) & r^2(\tilde{U}) K'(\tilde{T})/r_0 & r(\tilde{U}) K(\tilde{T}) r'(\tilde{U})/r_0 \\ -\alpha_1 \tilde{T} + \pi_1 \gamma_1 \tilde{U} & -\delta_0 - \alpha_1 \tilde{x} & \pi_1 \gamma_1 \tilde{x} \\ \alpha_1 \tilde{T} - \gamma_1 \tilde{U} & \alpha_1 \tilde{x} & -\gamma_1 \tilde{x} - \delta_1 \end{bmatrix}. \end{aligned}$$

Again,  $E_2$  is a hyperbolic saddle point, with a one-dimensional unstable and a two-dimensional stable manifold.

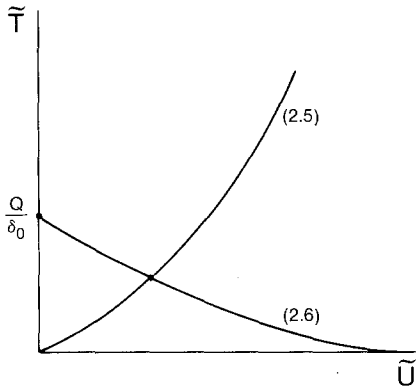


Fig. 1. The intersection of the graphs given by Eqs. (2.5) and (2.6). The intersection values form the  $\tilde{T}$  and  $\tilde{U}$  coordinates of  $\tilde{E}$

With respect to  $\tilde{E}$ , we are not able to show that it is always asymptotically stable. However, we are able to get sufficiency conditions for this property to hold.

**Theorem 2.2** *Let the following inequalities hold.*

$$2\alpha_1 \tilde{T} < r(\tilde{U}) + (1 + \pi_1)\gamma_1 \tilde{U} \tag{2.7a}$$

$$-r^2(\tilde{U})K'(\tilde{T}) < \delta_0 r_0 \tag{2.7b}$$

$$-r(\tilde{U})K(\tilde{T})r'(\tilde{U}) < r_0\gamma_1(1 - \pi_1)\tilde{x}_1 + r_0\delta_1. \tag{2.7c}$$

Then  $\tilde{E}$  is locally asymptotically stable.

*Proof.* If inequalities (2.7) hold, then by Gershgorin's theorem (Lancaster and Tismanetsky, 1985, p. 371), all eigenvalues of  $\tilde{M}$  have negative real parts, and the theorem follows.

In the following theorem, we are able to write down conditions which guarantee that  $\tilde{E}$  is globally stable. First we need a lemma which establishes the existence of a region of attraction for our system.

**Lemma 2.1** *The region*

$$\mathcal{A} = \{(x, T, U) : 0 \leq x \leq K_0, 0 \leq T + U \leq Q/\delta, \delta = \min(\delta_0, \delta_1)\}$$

*is a region of attraction.*

*Proof.* As before,  $\lim_{t \rightarrow \infty} x(t) \leq K_0$ , and  $\dot{T} + \dot{U} \leq -\delta(T + U) + Q$ . Hence  $\lim_{t \rightarrow \infty} [T(t) + U(t)] = Q/\delta$ , proving the lemma.

**Theorem 2.3** *In addition to assumptions (2.2) and (2.3), let  $r(U)$  and  $K(T)$  satisfy in  $\mathcal{A}$*

$$\begin{aligned} K_m \leq K(T) \leq K_0, \quad 0 \leq -K'(T) \leq \kappa \\ 0 \leq -r'(U) \leq \varrho, \end{aligned} \tag{2.8}$$

for some positive constants  $K_m, \kappa, \varrho$ . Then if the following inequalities hold

$$\left[ \frac{r_0 K_0 \kappa}{K_m^2} + \frac{\alpha_1 Q}{\delta} + \pi_1 \gamma_1 \tilde{U} \right]^2 < \frac{r_0}{K(\tilde{T})} (\delta_0 + \alpha_1 \tilde{x}) \quad (2.9a)$$

$$\left[ \varrho + \frac{\gamma_1 Q}{\delta} + \alpha_1 \tilde{T} \right]^2 < \frac{r_0}{K(\tilde{T})} (\delta_1 + \gamma_1 \tilde{x}) \quad (2.9b)$$

$$[\pi_1 \gamma_1 + \alpha_1]^2 K_0^2 < (\delta_0 + \alpha_1 \tilde{x})(\delta_1 + \gamma_1 \tilde{x}), \quad (2.9c)$$

$\tilde{E}$  is globally asymptotically stable with respect to solutions initiating in the interior of the positive orthant.

*Proof.* Since  $\mathcal{A}$  is an attracting region, and does not contain any invariant sets on the part of its boundary which intersects the interior of  $R_+^3$ , we restrict our attention to the interior of  $\mathcal{A}$ .

We consider the positive definite function about  $\tilde{E}$

$$V(x, T, U) = x - \tilde{x} - \tilde{x} \ln(x/\tilde{x}) + \frac{1}{2}(T - \tilde{T})^2 + \frac{1}{2}(U - \tilde{U})^2.$$

Then the derivative along solutions,  $\dot{V}$  is given by

$$\begin{aligned} \dot{V} = & \left(1 - \frac{\tilde{x}}{x}\right) x \left[ r(U) - \frac{r_0 x}{K(T)} \right] + (T - \tilde{T})[-\delta_0 T - \alpha_1 x T + \pi_1 \gamma_1 x U + Q] \\ & + (U - \tilde{U})[\alpha_1 x T - \gamma_1 x U - \delta_1 U]. \end{aligned}$$

After some algebraic manipulations, this can be written as

$$\begin{aligned} \dot{V} = & (x - \tilde{x}) \left[ r(\tilde{U}) - \frac{r_0 x}{K(\tilde{T})} \right] + (T - \tilde{T})[-\delta_0 T - \alpha_1 \tilde{x} T + \pi_1 \gamma_1 \tilde{x} \tilde{U} + Q] \\ & + (U - \tilde{U})[\alpha_1 \tilde{x} \tilde{T} - \gamma_1 \tilde{x} U - \delta_1 U] \\ & + [-r_0 x \xi(T) - \alpha_1 T + \pi_1 \gamma_1 \tilde{U}](x - \tilde{x})(T - \tilde{T}) \\ & + [\eta(U) + \alpha_1 \tilde{T} - \gamma_1 U](x - \tilde{x})(U - \tilde{U}) + [\pi_1 \gamma_1 + \alpha_1]x(T - \tilde{T})(U - \tilde{U}), \end{aligned}$$

where

$$\xi(T) = \begin{cases} \left( \frac{1}{K(T)} - \frac{1}{K(\tilde{T})} \right) / (T - \tilde{T}), & T \neq \tilde{T} \\ -\frac{K'(\tilde{T})}{K(\tilde{T})^2}, & T = \tilde{T} \end{cases} \quad (2.10a)$$

$$\eta(U) = \begin{cases} (r(U) - r(\tilde{U})) / (U - \tilde{U}), & U \neq \tilde{U}, \\ r'(\tilde{U}), & U = \tilde{U}. \end{cases} \quad (2.10b)$$

We note from (2.6) and the mean value theorem, that  $|\xi(T)| \leq \kappa / K_m^2$  and  $|\eta(U)| \leq \varrho$ .

We now note that

$$\begin{aligned} r(\tilde{U}) - \frac{r_0 x}{K(\tilde{T})} &= -\frac{r_0}{K(\tilde{T})}(x - \tilde{x}) \\ -\delta_0 T - \alpha_1 \tilde{x} T + \pi_1 \gamma_1 \tilde{x} \tilde{U} + Q &= -(\delta_0 + \alpha_1 \tilde{x})(T - \tilde{T}) \\ \alpha_1 \tilde{x} \tilde{T} - \gamma_1 \tilde{x} U - \delta_1 U &= -(\delta_1 + \gamma_1 \tilde{x}_1)(U - \tilde{U}). \end{aligned}$$



Hence  $\dot{V}$  can be written as the sum of three quadratic forms,

$$\begin{aligned}\dot{V} = & -\frac{1}{2}a_{11}(x - \tilde{x})^2 + a_{12}(x - \tilde{x})(T - \tilde{T}) - \frac{1}{2}a_{22}(T - \tilde{T})^2 \\ & -\frac{1}{2}a_{11}(x - \tilde{x})^2 + a_{13}(x - \tilde{x})(U - \tilde{U}) - \frac{1}{2}a_{33}(U - \tilde{U})^2 \\ & -\frac{1}{2}a_{22}(T - \tilde{T})^2 + a_{23}(T - \tilde{T})(U - \tilde{U}) - \frac{1}{2}a_{33}(U - \tilde{U})^2,\end{aligned}\quad (2.11)$$

where

$$\begin{aligned}a_{11} &= r_0/K(\tilde{T}), & a_{22} &= \delta_0 + \alpha_1 \tilde{x}, & a_{33} &= (\delta_1 + \gamma_1 \tilde{x}), \\ a_{12} &= -r_0 x \xi(T) - \alpha_1 T + \pi_1 \gamma_1 \tilde{U}, & a_{13} &= \eta(U) + \alpha_1 \tilde{T} - \gamma_1 U, \\ a_{23} &= (\pi_1 \gamma_1 + \alpha_1)x.\end{aligned}$$

Then a sufficient condition for  $\dot{V}$  to be negative definite is that

$$a_{12}^2 - a_{11}a_{22} < 0 \quad (2.12a)$$

$$a_{13}^2 - a_{11}a_{33} < 0 \quad (2.12b)$$

$$a_{23}^2 - a_{22}a_{33} < 0 \quad (2.12c)$$

hold. However (2.9a) implies (2.12a), (2.9b) implies (2.12b) and (2.9c) implies (2.12c). Hence  $\dot{V}$  is negative definite and so  $V$  is a Liapunov function with respect to  $\tilde{E}$ , whose domain contains  $\mathcal{A}$ , proving the theorem.

The above theorem shows, that provided inequalities (2.9) hold, the system settles down to a steady state of population (at a lower carrying capacity) and toxicant (at a level determined by influx and washout).

$$2.3 \quad f(t) = Q + \varepsilon\varphi(t), \quad \varphi(t + \omega) = \varphi(t)$$

In order to analyze system (2.1) in this case, we write it as

$$\dot{z} = F(z) + \varepsilon G(t), \quad z(0) = z_0, \quad (2.13)$$

where

$$z = \begin{pmatrix} z_1 \\ z_2 \\ z_3 \end{pmatrix} = \begin{pmatrix} x \\ T \\ U \end{pmatrix}, \quad F(z) = \begin{pmatrix} r(z_3)z_1 - r_0 z_1^2 / K(z_2) \\ -\delta_0 z_2 - \alpha_1 z_1 z_2 + \pi_1 \gamma_1 z_1 z_3 + Q \\ -\delta_1 z_3 + \alpha_1 z_1 z_2 - \gamma_1 z_1 z_3 \end{pmatrix}, \quad (2.14)$$

$$G(t) = \begin{pmatrix} 0 \\ \varphi(t) \\ 0 \end{pmatrix}, \quad z_0 = \begin{pmatrix} x_0 \\ T_0 \\ U_0 \end{pmatrix}.$$

Let  $z(t, \xi, \varepsilon)$  be the solution of Eq. (2.13) such that  $z(0, \xi, \varepsilon) = \tilde{z} + \xi$ , where

$$\tilde{z} = \begin{pmatrix} \tilde{x} \\ \tilde{T} \\ \tilde{U} \end{pmatrix}, \quad \xi = \begin{pmatrix} \xi_1 \\ \xi_2 \\ \xi_3 \end{pmatrix}.$$

Note that  $z(t, 0, 0) \equiv \tilde{z}$ .

We would like to establish the existence of a periodic solution of period  $\omega$  of system (2.13) for sufficiently small  $\varepsilon$ , which tends to  $\tilde{z}$  as  $\varepsilon \rightarrow 0$ . We will have done

so if we show that  $\xi$  can be chosen as a function of  $\varepsilon$  for  $\varepsilon$  small,  $\xi \rightarrow 0$  as  $\varepsilon \rightarrow 0$ , such that  $z(\omega, \xi, \varepsilon) = \tilde{z} + \xi$ .

With this in mind, we define

$$J(\xi, \varepsilon) = z(\omega, \xi, \varepsilon) - \tilde{z} - \xi. \quad (2.15)$$

If we can show that  $J(\xi, \varepsilon) = 0$  can be solved for  $\xi$  as a function of  $\varepsilon$ ,  $\xi(\varepsilon)$ , such that  $\xi(0) = 0$ , we will have shown the existence of a periodic solution. To do this we utilize the implicit function theorem (Freedman, 1968).

First we compute  $J(0, 0)$ . Now  $J(0, 0) = z(\omega, 0, 0) - \tilde{z} = \tilde{z} - \tilde{z} = 0$ . Then we must compute  $\det|J_\xi(0, 0)|$  and show that it is not zero. Now  $J_\xi(0, 0) = z_\xi(\omega, 0, 0) - I$ , where  $I$  is the identity matrix.

Using variational formulas, we have that  $z_\xi(t, \xi, \varepsilon)$  is the matrix solution of

$$\dot{z}_\xi(t, \xi, \varepsilon) = F_z(z(t, \xi, \varepsilon))z_\xi(t, \xi, \varepsilon), \quad z_\xi(0, \xi, \varepsilon) = I.$$

Hence setting  $\xi = 0, \varepsilon = 0$ , we get that  $z_\xi(t, 0, 0)$  is the matrix solution of

$$\dot{z}_\xi(t, 0, 0) = F_z(z(t, 0, 0))z_\xi(t, 0, 0), \quad z_\xi(0, 0, 0) = I.$$

But  $z(t, 0, 0) = \tilde{z}$  and  $F_z(\tilde{z}) = \tilde{M}$ . Hence

$$\dot{z}_\xi(t, 0, 0) = \tilde{M}z_\xi(t, 0, 0), \quad z_\xi(0, 0, 0) = I. \quad (2.16)$$

The solution of (2.16) is clearly

$$z_\xi(t, 0, 0) = e^{\tilde{M}t}, \quad (2.17)$$

and hence

$$J_\xi(0, 0) = e^{\tilde{M}\omega} - I. \quad (2.18)$$

This leads to the following theorem.

**Theorem 2.4** *If  $\tilde{M}$  has no eigenvalues with zero real parts, then system (2.1) with  $f(t) = Q + \varepsilon\varphi(t)$ ,  $\varphi(t + \omega) = \varphi(t)$  has a periodic solution of period  $\omega$ ,  $(x(t, \varepsilon), T(t, \varepsilon), U(t, \varepsilon))$  such that  $(x(t, 0), T(t, 0), U(t, 0)) = (\tilde{x}, \tilde{T}, \tilde{U})$ .*

*Proof.* If  $\tilde{M}$  has no eigenvalues with zero real parts, then 1 is not an eigenvalue of  $e^{\tilde{M}\omega}$ . This means that  $\det|J_\xi(0, 0) = \det|e^{\tilde{M}\omega} - I| \neq 0$ , and the theorem follows from the implicit function theorem.

**Corollary.** *If  $\tilde{M}$  has no eigenvalues with zero real parts, then for  $\varepsilon$  sufficiently small, the stability of the periodic solution is the same as the stability of  $\tilde{E}$ .*

*Proof.* This is clear since the periodic solution does not arise out of a bifurcation where stability changes can occur.

To complete the mathematical analysis of this section we show how to construct the periodic solution up to order of  $\varepsilon$ . In order to do this we need to compute the vector  $z_\varepsilon(t, 0, 0)$ .

First  $z_\varepsilon(t, \xi, \varepsilon)$  is the solution of

$$\dot{z}_\varepsilon(t, \xi, \varepsilon) = F_z(z(t, \xi, \varepsilon))z_\varepsilon(t, \xi, \varepsilon) + G(t), \quad z_\varepsilon(0, \xi, \varepsilon) = 0.$$

Hence  $z_\varepsilon(t, 0, 0)$  is given by the solution of

$$\dot{z}_\varepsilon(t, 0, 0) = \tilde{M}z_\varepsilon(t, 0, 0) + G(t), \quad z_\varepsilon(0, \xi, \varepsilon) = 0,$$

which is

$$z_\varepsilon(t, 0, 0) = e^{\tilde{M}t} \int_0^t e^{-\tilde{M}s} G(s) ds. \tag{2.19}$$

We now use Taylor series to write

$$z(t, \xi, \varepsilon) = \tilde{z} + z_\xi(t, 0, 0)\xi + z_\varepsilon(t, 0, 0)\varepsilon + \text{H.O.T.} \tag{2.20}$$

But  $\xi(\varepsilon) = \xi'(0)\varepsilon + o(\varepsilon)$ , where

$$\xi'(0) = -J_\xi(0, 0)^{-1} J_\varepsilon(0, 0) \quad \text{and} \quad J_\varepsilon(0, 0) = z_\varepsilon(\omega, 0, 0).$$

Hence  $\xi'(0) = -(e^{-\tilde{M}\omega} - I)^{-1} e^{\tilde{M}\omega} \int_0^\omega e^{-\tilde{M}s} G(s) ds$ . Then substituting all known functions into (2.20) gives

$$z(t, \xi, \varepsilon) = \tilde{z} + e^{\tilde{M}t} \left[ \int_0^t e^{-\tilde{M}s} G(s) ds - (e^{-\tilde{M}\omega} - I)^{-1} e^{\tilde{M}\omega} \int_0^\omega e^{-\tilde{M}s} G(s) ds \right] \varepsilon + o(\varepsilon). \tag{2.21}$$

### 3 Predator-prey

We develop our model by applying the same type of toxicant effects to a modified form of the intermediate predator-prey system discussed in Freedman (1987).

In addition to the assumptions made in the previous section, we assume that the predator functional response is decreased by the presence of toxin in the predator. As well, we assume that the predator death rate is toxin dependent, and that the ability of the predator to convert prey biomass into its own is also toxin dependent.

The toxin assumptions, in addition to those of the previous section are that toxin can enter the predator directly from the environment, or by consumption of prey. Toxin may leave the predator out of the system, or it may disperse back into the environment.

Hence if

$$\begin{aligned} x(t) &= \text{concentration of the prey biomass} \\ &= \frac{\text{mass (or volume) of the prey biomass}}{\text{mass (or volume) of the total environment}} \\ y(t) &= \text{concentration of the predator biomass} \\ &= \frac{\text{mass (or volume) of the predator biomass}}{\text{mass (or volume) of the total environment}} \\ T(t) &= \text{concentration of toxin in the environment} \\ &= \frac{\text{mass (or volume) of toxin in the environment} \\ &\quad \text{that is not in the predator or prey}}{\text{mass (or volume) of the total environment}} \\ U(t) &= \text{concentration of toxin in the prey} \\ &= \frac{\text{mass (or volume) of toxin in the prey}}{\text{mass (or volume) of the total environment}} \end{aligned}$$

$$V(t) = \text{concentration of toxin in the predator} \\ = \frac{\text{mass (or volume) of toxin in the predator}}{\text{mass (or volume) of the total environment}},$$

the model becomes

$$\begin{aligned} \dot{x} &= r(U)x - \frac{r_0 x^2}{K(T)} - yp(x, V) \\ \dot{y} &= y(-q(V) + c(V)p(x, V)) \\ \dot{T} &= -\delta_0 T - \alpha_1 xT - \alpha_2 yT + \pi_1 \gamma_1 xU + \pi_2 \gamma_2 yV + f(t) \\ \dot{U} &= -\delta_1 U + \alpha_1 xT - \gamma_1 xU - \beta(U)yp(x, V) \\ \dot{V} &= -\delta_2 V + \alpha_2 yT + \beta(U)yp(x, V) - \gamma_2 yV, \\ x(0) &= x_0 \geq 0, \quad y(0) = y_0 \geq 0, \quad T(0) = T_0 \geq 0, \quad U(0) = k_1 x_0, \\ V(0) &= k_2 y_0, \quad k_1, k_2 > 0 \end{aligned} \tag{3.1}$$

and have a similar interpretation as  $k$  of the previous section.

Here  $p(x, V)$  is the predator functional response,  $q(V)$  is the predator death rate,  $c(V)$  is the biomass conversion rate, and  $\beta(U)$  is the toxin transfer function. They satisfy the following hypotheses.

$$\begin{aligned} p(0, V) &= 0, \quad p_x(x, V) > 0, \quad p_V(x, V) < 0 \\ q(0) &= q_0 > 0, \quad q'(V) > 0 \\ c(0) &= c_0 > 0, \quad c'(V) < 0 \\ \beta(0) &= 0, \quad \beta'(U) > 0. \end{aligned} \tag{3.2}$$

Note that since we have not considered any delay effect in our model, it is assumed that the changes in population biomass, and toxin transfer through the environment to the population in a cyclic manner are instantaneous. It is implied that, though the population consists of individuals, the concentration of toxicant in them are changed instantaneously through the environmental chain (not from one individual to another, and hence the assumptions on  $\beta(U)$ ).

In the remainder of this section, we consider the same three functional forms for  $f(t)$  as in the previous section.

### 3.1 $f(t) \equiv 0$

In this case, we note that there are at most three equilibria, denoted  $F_0(0, 0, 0, 0, 0)$ ,  $F_1(K_0, 0, 0, 0, 0)$  and  $\hat{F}(\hat{x}, \hat{y}, 0, 0, 0)$ .  $F_0$  and  $F_1$  always exist.  $\hat{F}$  exists and is globally stable in the positive  $xy$  quadrant if and only if there exists  $\hat{x} < K_0 \equiv K(0)$  such that  $p(\hat{x}, 0) = q(0)/c(0)$  (Freedman, 1987). Noting that

$$\dot{T} + \dot{U} + \dot{V} = -\delta_0 T - \delta_1 U - \delta_2 V - (1 - \pi_1)\gamma_1 xU - (1 - \pi_2)\gamma_2 xV < 0 \tag{3.3}$$

then  $\lim_{t \rightarrow \infty} (T + U + V) = 0$ . Hence if  $\hat{F}$  exists, it is globally asymptotically stable, with respect to the positive orthant. If  $\hat{F}$  does not exist, then  $F_1$  is globally asymptotically stable.  $F_0$  is always unstable.

3.2  $f(t) \equiv Q$

In this case, there are always equilibria of the form  $F_2(0, 0, Q/\delta_0, 0, 0)$ , which is unstable, and  $\tilde{F}(\tilde{x}, 0, \tilde{T}, \tilde{U}, 0)$  where  $\tilde{x}, \tilde{T}, \tilde{U}$  are determined from the previous section. However, the question of whether or not one or more positive equilibria of the form  $F^*(x^*, y^*, T^*, U^*, V^*)$  exists is not easily answered. In general, one would need to show that there exists a positive solution to the system of algebraic equations

$$\begin{aligned} r(U)x - \frac{r_0x^2}{K(T)} - yp(x, V) &= 0 \\ -q(V) + c(V)p(x, V) &= 0 \\ -\delta_0T - \alpha_1xT - \alpha_2yT + \pi_1\gamma_1xU + \pi_2\gamma_2yV + Q &= 0 \\ -\delta_1U + \alpha_1xT - \gamma_1xU - \beta(U)yp(x, V) &= 0 \\ -\delta_2V + \alpha_2yT + \beta(U)yp(x, U) - \gamma_2yV &= 0. \end{aligned} \tag{3.4}$$

In general we are unable to do so.

However, we are able to show the existence of  $F^*$  in two cases and determine its stability in one of them.

Firstly, if  $\tilde{F}$  is globally asymptotically stable in  $x$ - $T$ - $U$  space, and unstable locally in the  $y$  direction, and is furthermore hyperbolic, then using the persistence results described in Butler, Freedman and Waltman (1986) and in Freedman and So (1985), we can conclude that  $F^*$  exists, but cannot determine its stability.

The second case is the case that  $Q$  is so small, that we may think of system (3.4) as a perturbation of the same system with  $Q = 0$ . Then we can show the existence of  $F^*$  for sufficiently small  $Q$  by the implicit function theorem.

To this end, let

$$H(x, y, T, U, V, Q) = \begin{pmatrix} r(U)x - r_0x^2/K_1(T) - yp(x, V) \\ -q(V) + c(V)p(x, V) \\ -\delta_0T - \alpha_1xT - \alpha_2yT + \pi_1\gamma_1xU + \pi_2\gamma_2yV + Q \\ -\delta_1U + \alpha_1xT - \gamma_1xU - \beta(U)yp(x, V) \\ -\delta_2V + \alpha_2yT + \beta(U)yp(x, V) - \gamma_2yV \end{pmatrix} \tag{3.5}$$

Then  $H(\hat{x}, \hat{y}, 0, 0, 0) = 0$ . Hence we would like to determine whether or not  $H(x, y, T, U, V, Q) = 0$  can be solved for  $x, y, T, U, V$  as function of  $Q$  near  $x = \hat{x}, y = \hat{y}, T = U = V = 0$ . If we let

$$w = \begin{pmatrix} x \\ y \\ T \\ U \\ V \end{pmatrix}, \quad \hat{w} = \begin{pmatrix} \hat{x} \\ \hat{y} \\ 0 \\ 0 \\ 0 \end{pmatrix},$$

then the Jacobian matrix  $H_w|_{w=\hat{w}} \equiv \hat{H}_w$  is computed as

$$\hat{H}_w = \begin{bmatrix} \hat{L}_{11} & \hat{L}_{12} \\ O_{32} & \hat{L}_{22} \end{bmatrix},$$

where

$$\hat{L}_{11} = \begin{bmatrix} r_0 - 2r_0\hat{x}/K_0 - \hat{y}p_x(\hat{x}, 0) & -p(\hat{x}, 0) \\ c(0)p_x(\hat{x}, 0) & 0 \end{bmatrix}$$

$$\hat{L}_{12} = \begin{bmatrix} r_0\hat{x}^2K'(0)/K_0^2 & r'(0)\hat{x} & -\hat{y}p_v(\hat{x}, 0) \\ 0 & 0 & -q'(0) + c(0)p_v(\hat{x}, 0) + c'(0)p(\hat{x}, 0) \end{bmatrix}$$

$$\hat{L}_{22} = \begin{bmatrix} -\delta_0 - \alpha_1\hat{x} - \alpha_2\hat{y} & \pi_1\gamma_1\hat{x} & \pi_2\gamma_2\hat{y} \\ \alpha_1\hat{x} & -\gamma_1\hat{x} - \delta_1 - \beta'(0)\hat{y}p(\hat{x}, 0) & 0 \\ \alpha_2\hat{y} & \beta'(0)\hat{y}p(\hat{x}, 0) & -\gamma_2\hat{y} - \delta_2 \end{bmatrix},$$

$O_{32}$  is the  $3 \times 2$  zero matrix. From the structure of  $\hat{H}_w$ , we see that  $\det \hat{H}_w = (\det \hat{L}_{11})(\det \hat{L}_{22})$ .

We can now state and prove our result.

**Theorem 3.1** *If  $\hat{F}$  exists, then  $F^*$  exists for sufficiently small  $Q > 0$ , and is asymptotically stable.*

*Proof.* To show the existence of an equilibrium for small  $Q$ , from the above considerations, we need only conclude that  $\det \hat{H}_w = (\det \hat{L}_{11})(\det \hat{L}_{22}) \neq 0$ .  $\det \hat{L}_{11} = c(0)p(\hat{x}, 0)p_x(\hat{x}, 0) > 0$ . To show that  $\det \hat{L}_{22} \neq 0$ , we again utilize the Gershgorin circles, using columns of  $\hat{L}_{22}$ . For the first column, the centre is at  $(-\delta_0 - \alpha_1\hat{x} - \alpha_2\hat{y}, 0)$  of the complex plane, and the radius is  $\alpha_1\hat{x} + \alpha_2\hat{y} < \delta_0 + \alpha_1\hat{x} + \alpha_2\hat{y}$ . Hence the circle lies to the left of the imaginary axis. Since  $\beta'(0) > 0$  and  $0 \leq \pi_i \leq 1$ ,  $i = 1, 2$ , the same can be said for the other two Gershgorin circles. Hence all three eigenvalues of  $\hat{L}_{22}$  have negative real parts and therefore  $\det \hat{L}_{22} \neq 0$ .

Hence, by the implicit function theorem,  $H(x, y, T, U, V, Q) = 0$  can be solved for  $w$  as a function of  $Q$  in a neighborhood of  $w = \hat{w}$ ,  $Q = 0$ , in the form

$$w(Q) = \hat{w} - \hat{H}_w^{-1} \hat{H}_Q Q + o(Q), \quad (3.6)$$

where  $\hat{H}_Q \equiv H_Q|_{w=\hat{w}, Q=0}$ . We see from (3.5) that

$$\hat{H}_Q = \begin{bmatrix} 0 \\ 0 \\ 1 \\ 0 \\ 0 \\ 0 \end{bmatrix}.$$

Since  $\hat{x} > 0$  and  $\hat{y} > 0$ , then for  $Q$  sufficiently small,  $x^*(Q) > 0$  and  $y^*(Q) > 0$ . We now wish to show that  $T^*(Q)$ ,  $U^*(Q)$  and  $V^*(Q)$  are positive as well for  $Q$  positive and small so that  $F^*$  will exist.

From (3.6) we can note that

$$\begin{aligned} \frac{dT^*}{dQ}(0) &= -(\hat{H}_w^{-1})_{33} \\ &= \frac{-(\det \hat{L}_{11}) \det \begin{pmatrix} -\gamma_1\hat{x} - \delta_1 - \beta'(0)\hat{y}p(\hat{x}, 0) & 0 \\ \beta'(0)\hat{y}p(\hat{x}, 0) & -\gamma_1\hat{y} - \delta_2 \end{pmatrix}}{(\det \hat{L}_{11})(\det \hat{L}_{22})}. \end{aligned}$$

Now since the eigenvalues of  $\hat{L}_{22}$  are in fact negative,  $\det \hat{L}_{22} < 0$ .

Hence  $\text{sgn}(dT^*/dQ)(0) = \text{sgn}(\gamma_1 \hat{x} + \delta_1 + \beta'(0)\hat{y}p(\hat{x}, 0))(\gamma_2 \hat{y} + \delta_2) > 0$ , i.e.  $(dT^*/dQ)(0) > 0$ . Similarly, we can show that  $(dU^*/dQ)(0) > 0$  and  $(dV^*/dQ)(0) > 0$ . Hence  $T^*(Q) = (dT^*/dQ)(0)Q + o(Q) > 0$  for sufficiently small  $Q > 0$ . Similarly  $U^*(Q) > 0$  and  $V^*(Q) > 0$  for small, positive  $Q$  and so  $F^*$  exists.

Finally, the stability of  $F^*$  is the same as the stability of  $\tilde{F}$  since only a perturbation and not a bifurcation occurs, proving the theorem.

$$3.3 \quad f(t) = Q + \varepsilon\varphi(t), \quad \varphi(t + \omega) = \varphi(t)$$

In this case, the analysis is similar to that of Sect. 2.3. If  $F^*$  exists when  $\varepsilon = 0$ , then a periodic solution of small amplitude exists when  $\varepsilon$  is sufficiently small, and its stability is the same as that of  $F^*$  in the hyperbolic case.

#### 4 Discussion

In this paper, we have described modes representing the effects of a toxin introduced into the environment of single-species and predator-prey systems. The single-species growth model is of a modified logistic form. We have allowed for a general predator functional response in the predator-prey model.

We have only considered cases where the toxin at any level will wash out of the environment at some rate (perhaps small) whether the toxin is free in the environment, or contained within a population. Such an assumption is valid, for example, in stream dynamics, lake dynamics, forest dynamics, etc.

For each model, we have considered three cases, namely, when there is a single introduction of toxin, a constant introduction, and a periodic introduction.

In both models in the case of a single introduction, we have shown that the toxin eventually washes out of the environment in its totality. This agrees with our intuition. Of course, the time for this to occur could be very long if the washout rates are small.

In the case of a constant influx of toxin, we have shown that the single-species population can be expected in many cases to settle down to a steady state. We have actually obtained criteria for the asymptotic stability and even the global stability for this steady state. We note that as expected, the criteria for global stability are more stringent than the criteria for local stability, since the former criteria involve inequalities which must be satisfied in a region, and the later criteria involve inequalities to be satisfied at one point.

In the periodic case, we have shown that a small periodic influx of toxin induces a periodic behaviour in the population dynamics. This is not surprising if one thinks of the toxin as influencing the carrying capacity of the environment.

In the predator-prey case with constant influx of toxicant, the existence and stability of a positive equilibrium in general is an open problem. For both models, the existence of periodic solutions for general period influxes of toxicant is also open for discussion.

Our models can be generalized in obvious ways to food chains and competitive systems. In particular, the question of reversal of outcome for competitive systems due to the presence of toxin is of great interest. These questions are left to future research.

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