Stability of a Population in a Model with Delayed Environmental Response

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Abstract: We present a theoretical analysis of the temporal variation of a population subject to a variable environment. This is achieved by treating the carrying capacity, a proxy for the environment as a state-variable. This enables us to describe the population and environment interaction via a set of nonlinear coupled differential equations. Importantly, we discuss the effect of a delay in the environmental response to changes in population density. The existence of a Hopf bifurcation is established as well as the minimum time delay required for the onset of sustained periodic fluctuations in the population. Finally, we discuss the ecological management implications imputed by the model.

Key words: Carrying capacity, delay differential equation, logistic equation, predator-prey model, fluctuation

INTRODUCTION

The logistic equation, despite its limitations, has been widely applied in population and ecological modelling. The classical logistic equation for a single population of density N(t) is characterized by:

$$\frac{dN}{dt} = aN(t)\left(1 - \frac{N(t)}{K_0}\right), N(0) = N_0 \qquad (1)$$

Where:
N_0 = The initial population density
a = The intrinsic growth rate
K_0 = The constant carrying capacity

The expression a $(1-N/K_0)$ represents a density dependent growth rate which ensures that growth is a self-limiting process. The logistic equation, introduced by Verhulst is a modification to the Malthusian Model which predicts an exponential increase in population unrestrained by resources and without predation (Agarwal *et al.*, 2014). However, due to environmental limitations that is the shortage of resources and space, the presence of natural predators, impose limitations on the size of the population that can be sustained.

The carrying capacity, K_0 in Eq. 1 is usually considered to be fixed which does not realistically represent the state of an environment or habitat. Early attempts to incorporate seasonal effects into models were the inclusion of a time-varying carrying capacity

(Rogovchenko and Rogovchenko, 2009). Subsequently, other time dependent functional forms of the carrying capacity were proposed to describe different environmental changes. A saturating functional form was used to model microbial growth under an occlusion of healthy human skin (Safuan *et al.*, 2011). A logistically varying carrying capacity has been used to model the role of technological advances in the increase of the human population (Meyer, 1994; Meyer and Ausubel, 1999).

More recently, the carrying capacity was considered as a state-variable, thus described by a differential equation. An extensive study has been done on the importance and relevance of treating the carrying capacity as a proxy for the state of the environment (Safuan *et al.*, 2013).

In most cases, the growth and maintenance of a population is controlled by environmental limitations which themselves are subject to variations due to both exogenic and endogenic processes. A population can grow exponentially or fluctuate, even exhibit chaotic dynamics, depending on environmental conditions (Becks *et al.*, 2005). The feedback about the state of the environment, via the carrying capacity, may show delays due to the complex interactions between the population and its environment (Saether, 1997).

A delay is incorporated into the logistic equation for capturing oscillations that are apparent in Daphnia populations (Hutchinson, 1948). More recently, a delayed system of equations was successfully used to model the

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irruptive dynamics of large herbivores subject to changes in their food supply (Forsyth and Caley, 2006). The consumption of available food by the herbivores was considered as environmental stress and thus modeled via induced changes in the carrying capacity.

The interaction between a population and its biotic resource (food) may exhibit delays as the resource modifies its internal process to adjust to the presence of the population. A delay may be directly incorporated into the carrying capacity in the logistic equation to describe the growth of a population (Yukalov *et al.*, 2009). In this study, a delay is included into the rate equation for the carrying capacity. The dynamics of the population and a bifurcation analysis are presented.

Coupled delayed logistic carrying capacity model: It is well established that herbivory has a detrimental effect on flora growth and development (Saether, 1997). In New Zealand, possum browsing causes defoliation that inhibits or reduces flowering and fruiting of affected trees and plants. When possum numbers are reduced, such trees and plants flowered and fruited abundantly (Cowan and Waddington, 1990). A model that describes this observed effect of possum browsing is given by Safuan *et al.* (2012):

$$\frac{dN}{dt} = aN(t)\left(1 - \frac{N(t)}{K(t)}\right) \qquad (2)$$

$$\frac{dK}{dt} = dK(t) - cK(t)N(t) \qquad (3)$$

This important class of models directly couples the rate of change in the population to the rate of change in the abundance of a biotic resource upon which the population depends on (the environment). Here a is the intrinsic growth rate of the population, b the intrinsic growth rate of the biotic environment and c is a measure of the intensity of consumption of the biotic resource by the population. Equation 2 can also be written as $K(t) = R_K(N) K$ where $R_K(N) = b-cN$ represents a density-dependent replenishment rate. It is important to note that N depends on $R_K(N)$, this implies that the presence of the population alters the rate at which the biotic resource replenishes.

System of Eq. 3 can be non-dimensionalized under the change of variables, $N^* = cN/b$, $K^* = cK/b$, $t^* = at$, then dropping the Asterisk (*) yields:

$$\frac{dN}{dt} = N(t)\left(1 - \frac{N(t)}{K(t)}\right) \qquad (4)$$

$$\frac{dK}{dt} = \mu(1 - N(t))K(t) \qquad (5)$$

where, $\mu = b/a$. This system has a stable equilibrium solution at $(N_e, K_e) = (1, 1)$. Whenever $0<N<1$, the rescaled $R_K(N) = \mu(1-N(t))$ remains positive and thus the resource is increasing. Whenever, $N>1$ then $R_K(N)<0$, so the biotic resource is decreasing. The value of μ is a key parameter. If $\mu<0.25$ then $N<1$ for all t. As $N\rightarrow1$, $R_K(N)\rightarrow0$ asymptotically reaching the equilibrium solution. However, if $\mu>0.25$ and for N small, the resource increases rapidly and overshoots the equilibrium value $K_e = 1$. According to Eq. 2 the population N follows K. When $N>1$, then $R_K(N)<0$ thus reducing the available resource, causing the population to also decrease. As the resource decreases it passes through K_e and when N drops below N_e then $R_K(N)>0$ halting the decrease in resources and is then followed by an increase again. This results in a periodic behavior with exponentially decreasing amplitude until equilibrium is achieved.

In Eq. 4 and 5, the rescaled $R_K(N)$ changes instantaneously with the population N at time t. We propose a model where the effect on the replenishment rate of the biotic resource exhibits a delay in response to its consumption by the population. Returning to the example of possum browsing of fruiting trees and plants, the flowers have a long developmental period which could be modeled by the inclusion of a delay. The model with delay is:

$$\frac{dN}{dt} = N(t)\left(1 - \frac{N(t)}{K(t)}\right) \qquad (6)$$

$$\frac{dK}{dt} = \mu(1 - N(t-t))K(t) \qquad (7)$$

Now $R_K(N) = \mu(1-N(t-\tau))$ where τ is some characteristic feature that measures the delayed response of the biotic resource to its consumption. The effect of τ on the model dynamics is analysed.

Local stability analysis: In this section, we first derive the equilibrium solution of Eq. 6 and 7 then linearize around the equilibrium solution to determine its stability. We show the existence of limit cycles when the delay is above some critical value.

Let the equilibrium solution again be denoted by (N_e, K_e). Then, setting the right-hand side of Eq. 6 and 7 to zero with the substitutions $N(t) = N(t-\tau) = N_e$ and $K(t) = K_e$ we find the equilibrium solution to be (1, 1) as before. To linearize around the equilibrium solution we write $N(t) = 1+n(t)$ and $K(t) = 1+k(t)$ where both n(t)

and K(t) are small perturbations. Substituting into Eq. 6 and 7 retaining only linear terms in n(t), k(t) and K(t) leads to the linearized system:

$$\frac{dn}{dt} = -n(t) + k(t) \tag{8}$$

$$\frac{dk}{dt} = -\mu n(t - \tau) \tag{9}$$

We assume the solutions for both n(t) and K(t) can be written as $e^{\lambda t}$ leading to the characteristic equation:

$$\lambda'^2 + \lambda + \mu e^{-\lambda t} = 0 \tag{10}$$

Setting $\tau = 0$ in Eq. 6 reduces to that for the non-delay model (Safuan *et al.*, 2012). Equation 10 may have real or complex roots depending on the values of μ and τ.

Figure 1 identifies three distinct regions in the (μ, τ) parameter space categorised by the nature the roots of Eq. 10. In Region 1, both roots are real and negative indicating that (1,1) is a stable equilibrium solution. In Region 2, both roots lie on the left-half of the complex the plane. This results in oscillating solutions about the equilibrium with exponentially decaying amplitudes. On the boundary of Region 1 and 2, there is a single (degenerate) negative root. Unlike, the previous two regions, in Region 3 the roots of Eq. 10 are now complex with positive real parts. The solutions are locally unstable. Purely imaginary roots occur on the boundary of Regions 2 and 3. By crossing this boundary, the stability changes, thus representing a bifurcation of the solution.

We can determine the conditions for which bifurcation occurs by substituting $\lambda = i\omega$ into Eq. 10. Then, setting the real and imaginary parts to zero leads to Eq. 11 and 12:

$$\mu \cos(\omega \tau) - \omega^2 = 0 \tag{11}$$

$$\omega - \mu \sin(\omega \tau) = 0 \tag{12}$$

Solving for the critical values ω_c and τ_c we obtain:

$$\omega_c^2 = \frac{\sqrt{1 + 4\mu^2} - 1}{2} \tag{13}$$

$$\tau_c = \frac{1}{\omega_c} \tan^{-1}\left(\frac{1}{\omega_c}\right) + \frac{\pi i}{\omega_c}, \text{ for } i = 0, 1, 2, \ldots \tag{14}$$

Furthermore and with reference to Fig. 1, for μ fixed and in vicinity of the bifurcation curve, as τ crosses the
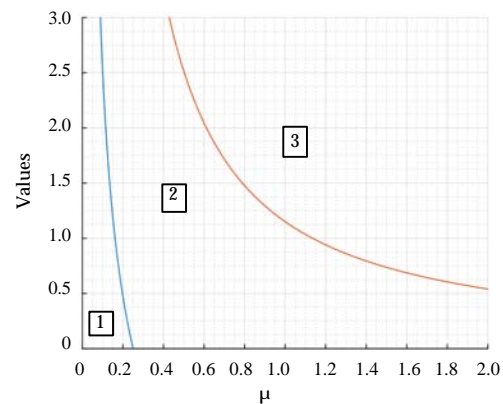

Fig. 1: Regions in the (μ, τ) parameter space denoting the different types of roots of the characteristic equation. In Region 1, all of the roots are real and negative. In Region 2, all of the roots lie on the left-half of the complex plane. In Region 3, all of the roots lie on the right-half of the complex plain. On the boundary of Region 2 and 3 the roots are purely imaginary

bifurcation curve from Region 2 into region III the transversal condition $R\{d\lambda/d\tau\} > 0$ is satisfied which is a necessary condition for the existence of a Hopf bifurcation. In this instance the bifurcation is supercritical.

RESULTS AND DISCUSSION

Unlike, the non-delayed model Eq. 4 and 5, the proposed delayed model Eq. 6 and 7 undergoes a Hopf bifurcation leading to the formation of a limit cycle once τ exceeds the minimum critical value τ_c. However, τ_c varies as the parameter μ varies.

Figure 2 compares the solutions of Eq. 3 to those of Eq. 4. The left panel shows the time evolution of both $N(\tau)$ and K(t) whereas the right panel shows the corresponding phase-plane. For all cases we have fixed t = 1.5 whereas, μ is chosen from each of the Regions 1-3. The initial conditions for the system Eq. 4 and 5 are (N(0), K(0) = 0.1, 0.1) while for the delayed system (4) the history functions are N(t) = 0.1, t∈[-τ, 0] and K(0) = 0.1.

For Region 1, we take $\mu = 0.15(\mu < 1/4)$. Figure 2a shows the time evolution of the population (solid lines) for both the non-delayed system (Eq. 4 and 5) (blue) and the delayed system (Eq. 6 and 7) (red) and their corresponding carrying capacities (dashed lines). The population monotonically approaches the equilibrium solution.

Figures 2c and d illustrate the effect of a delay within Region 2. For the case $\mu = 0.6$ ($\mu < 1/4$) the notable feature in the numerical solutions are the damped oscillations in
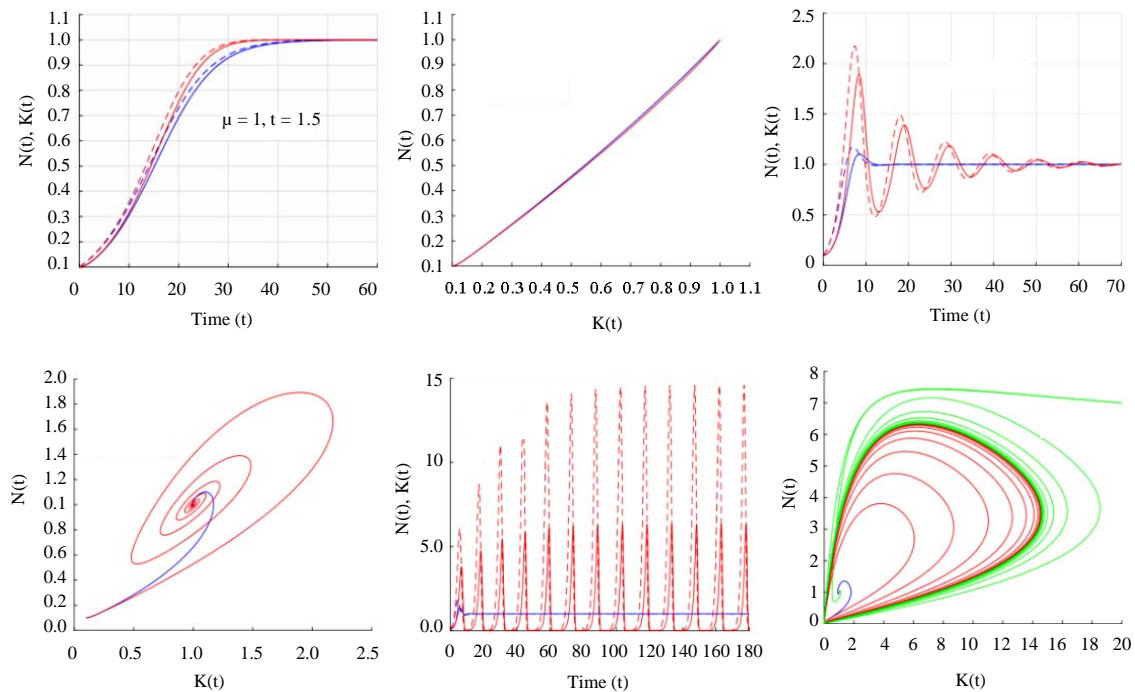
Fig. 2: Numerical solutions for the non-delay and delay models. The left column depicts the time evolution of the populations and their carrying capacities for different values of µ with τ = 1.5 The right column shows the corresponding phase plots. Blue curves represent the non-delayed system and the red curves represent the delayed system. Carrying capacities are represented by dashed lines and the populations are represented by solid lines

the population and the carrying capacity for both models. For the delayed model, the amplitude of oscillations are larger compared to the non-delayed model for the same µ. By increasing µ but wholly remaining within Region 2, the oscillations persist longer as we approach the boundary of theHopf bifurcation locus.

Next we consider the case for µ = 1 that is when the intrinsic growth rate of the biotic resource is equal to the population growth rate. As µ>0.25 system Eq. 4 and 5 exhibits damped oscillations about its equilibrium solution. However, system Eq. 6and 7 undergoes a Hopf bifurcation due of the choice of µ and τ being in Region 3 of Fig. 1. In this situation, the amplitude of the oscillations increase or decrease depending on the history functions before reaching the limit cycle. This behavior is clearly depicted in Fig. 2f. Solutions of the delayed system (red curve) with history functions located inside the limit cycle spiral outwards and asymptotically approach the stable limit cycle. Similarly, solutions (green curve) with history functions located outside the limit cycle are attracted inward and towards the limit cycle.

CONCLUSION

We have previously proposed a model to describe the interaction of a population with its environment (Safuan *et al.*, 2012). The environment is represented as a biotic resource which sustains the population. As the population consumes the resource, it alters the environment by reducing the rate of replenishment of the resource. Here we include a delay in the response of the environment to changes in the population density. For delays below the minimum threshold, τ_c the population approaches its equilibrium. For delays above τ_c the environment and the population exhibit periodic oscillations. The amplitude of the oscillations in the carrying capacity, a measure of the variability in the biotic resource, is much larger than that of the population. This feature is built into the delayed model (Eq. 4 and 7).

From the differential equation for N(t) we have: $N'(t)<0$ if $K(t)<N(t)$; $N'(t)>0$ if $K(t)>N(t)$. This means that N(t) will tend to follow K(t) when K(t) is higher N(t) will increase towards K(t) and when K(t) is lower N(t) will decrease towards K(t). In the case where the intrinsic

growth rate a is large (μ is small), the rate of change of N(t) will be large in magnitude so that it will follow K(t) closely. The solution for N(t) shows smaller amplitudes for smaller values of a (larger values of μ) the population is less affected by rapid changes to the carrying capacity. Figure 2e illustrates that delays can induce large amplitude oscillations in the carrying capacity as well as in the population. Of concern is the very low population density during the lower end of the cycle. A low population density is vulnerable to environmental stochastic perturbations which are ever present. It is then of vital importance to appropriately manage such a situation to ensure that oscillations are reduced or eliminated altogether.

Depending on the situation, the harvesting of the population may be the only option to consider. When to harvest and the intensity of the harvest are important considerations. In many circumstances maintaining a constant harvesting policy might be appropriate but it might be more cost effective for frequent short-term harvesting.

Finally, we may never be able to accurately predict long-term population dynamics until we understand the impact of populations on the environment, for example the effect of browsing on plant physiological, changes in demographic parameters, the influence of vegetation abundance and nutritional quality on population fecundity. All of these interactions require further consideration.

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