

1-2-2017

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Recommended Citation

Mickens, Ronald E.; Harlemon, Maxine; and Oyedeji, Kale, "Consequences of Culling in Deterministic ODE Predator-Prey Models" (2017). *Morehouse Faculty Publications*. 19.
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Consequences of Culling in Deterministic ODE Predator-Prey Models*

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January 12, 2017

Abstract

We show, within the context of the standard class of deterministic ODE predator-prey mathematical models, that predator culling does not produce a long term decrease in the predator population.

Keywords: Predator-prey models; Mathematical ecology; Culling; Stability of fixed points.

AMS Subject Classification: 34C05, 34D20, 92D40

1 Introduction

Consider the interactions between predator, $y(t)$ and prey, $x(t)$, populations. The time variable, t , is explicitly shown since both populations are expected to change with time.

Now define culling as the external reduction of the predator population at time, $t = t_0$, by an amount y_c , i.e.,

$$y(t_0) \rightarrow y(t_0) - y_c, \quad (1.1)$$

where

$$0 < y_c < y(t_0). \quad (1.2)$$

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Generally, this is done with the expectation that there will be a (long term) corresponding increase in the prey population. This action may be repeated into the future at either regular or irregular time intervals.

The purpose of this work is to provide arguments which show that within the context of standard mathematical predator-prey (P-P) models, based on coupled ordinary differential equations, culling does not change the long term behavior/values of either the predator or prey populations. This (almost) obvious and important consequence for this class of models is generally not fully understood and appreciated within the framework of population dynamic calculations.

Our interest in the topic of predator culling had its genesis in the NEWS in Depth story, “No proof that predator culls save livestock, study claims,” by Goldfarb [2]. He presented evidence which indicates that the outcomes of predator culling may not be consistent with prior notions of what should occur, namely, an end or at least a reduction in predation. Our conclusion is that the net effect of culling, again within the standard ODE P-P mathematical modelling is zero, as stated in the previous paragraph.

The paper is organized as follows: Section 2 lists a number of the better known P-P models. This is done to provide an indication of the broad range of mathematical structures which have been constructed for P-P interactions. Section 3 gives a summary of the generic properties expected of a P-P model and, in particular, the important feature of the nontrivial fixed-point, i.e., the constant solutions

$$x(t) = \bar{x} > 0, \quad y(t) = \bar{y} > 0, \quad (1.3)$$

where the prey and predator can mutually exist. Section 4 is the center of the paper. There, we discuss and derive the main conclusion, i.e., culling does not lead to the desired outcome within the frame work of deterministic ODE models. We end, in Section 5, by briefly discussing other mathematical models for which the conclusions of this paper may not hold.

2 ODE Based P-P Models

Below are listed five P-P mathematical models based on their formulation in terms of coupled, nonlinear ODE's. Note, we only consider the case for which there is a single prey population, $x(t)$, and a single predator population, $y(t)$.

The references [4, 5, 7, 8] provide background historical information on these and other P-P models as well as giving, in several cases, associated analytical and numerical analyses. It should be noted that the non-negative

parameters, (a, b, c, d, r, K, g) may, in different equations have different physical units, as well as different interpretations as to their ecological meaning.

We now give a representative listing of P-P models which have been studied:

Lotka-Volterra

$$\frac{dx}{dt} = x(a - by), \quad \frac{dy}{dt} = y(-c + dy), \quad (2.1)$$

Verhulst-Pearl (Logistic)

$$\frac{dx}{dt} = rx(K - x) - bxy, \quad \frac{dy}{dt} = y(-c + dy). \quad (2.2)$$

Gompertz

$$\frac{dx}{dt} = rx \operatorname{Ln} \left(\frac{K}{x} \right) - bxy, \quad \frac{dy}{dt} = y(-c + dy). \quad (2.3)$$

Logistic-Ivlev

$$\frac{dx}{dt} = rx(K - x) - y[1 - \exp(-bx)], \quad (2.4a)$$

$$\frac{dy}{dt} = y \{-c + d[1 - \exp(-bx)]\}. \quad (2.4b)$$

Logistic-Holling-Leslie

$$\frac{dx}{dt} = rx(K - x) - \frac{axy}{b + x}, \quad (2.5a)$$

$$\frac{dy}{dt} = cy \left[1 - \left(\frac{y}{gx} \right) \right] \quad (2.5b)$$

An examination of the book by May [5] allows one to see how many other ODE based models can be constructed for P-P interactions.

3 Generic Properties of P-P Models

Realistic ODE based mathematical models of P-P interactions should have certain features. If we write

$$\frac{dx}{dt} = xF(x, y), \quad \frac{dy}{dt} = yG(x, y), \quad (3.1)$$

where $x(t)$ and $y(t)$ are the respective prey and predator populations, then in the (x, y) phase-space [6, 7], Eqs. (3.1) must have (at least) three fixed-points (FP), also known as constant or equilibrium solutions, to be a valid model of a P-P system. If we denote a FP by the notation (\bar{x}, \bar{y}) , then a minimal PP model

(i) has a FP at $(\bar{x}^{(1)}, \bar{y}^{(1)}) = (0, 0)$. This corresponds to a state for which there are no prey or predators.

(ii) has a FP at $(\bar{x}^{(2)}, \bar{y}^{(2)}) = (\bar{x}, 0)$. For this state, there are no predators, but the prey can exist by itself at the equilibrium value $x(t) = \bar{x}$.

(iii) has a nontrivial FP at $(\bar{x}^{(3)}, \bar{y}^{(3)}) = (x^*, y^*)$, where the prey and predator can co-exist.

These three cases are shown in Figure 1. However, detailed investigation of these cases allows the following conclusions to be reached [3, 4, 5, 7, 8]:

(a) The FP's at $A = (0, 0)$ and $B = (\bar{x}, 0)$ are locally unstable.

(b) The FP at $C = (x^*, y^*)$ can have three types of stability [6]: neutral stability, corresponding to a center; a stable node, or an unstable node.

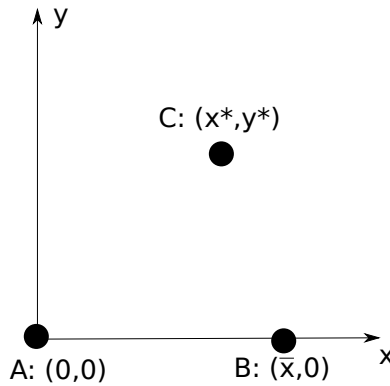


Figure 1: The location of the fixed-points (FP) for a generic P-P system. FP-A is unstable. FP-B is unstable. FP-C may have neutral stability, i.e., it is a center, be a stable node, or be an unstable node.

Since our major interest is FP-C, we illustrate in Figure 2, the outcomes of the three cases listed in (b). Note that the case for the center is not realistic since one can select initial conditions, $x(0) = x_0 > 0$ and $y(0) = y_0 > 0$, such that the predator and prey oscillation amplitudes can be arbitrarily (but finite) large. Consequently, this implies that the Lotka-Volterra model, see Eq. (2.1), while widely used to illustrate P-P dynamics, is not realistic. We will not consider this case any further in this paper.

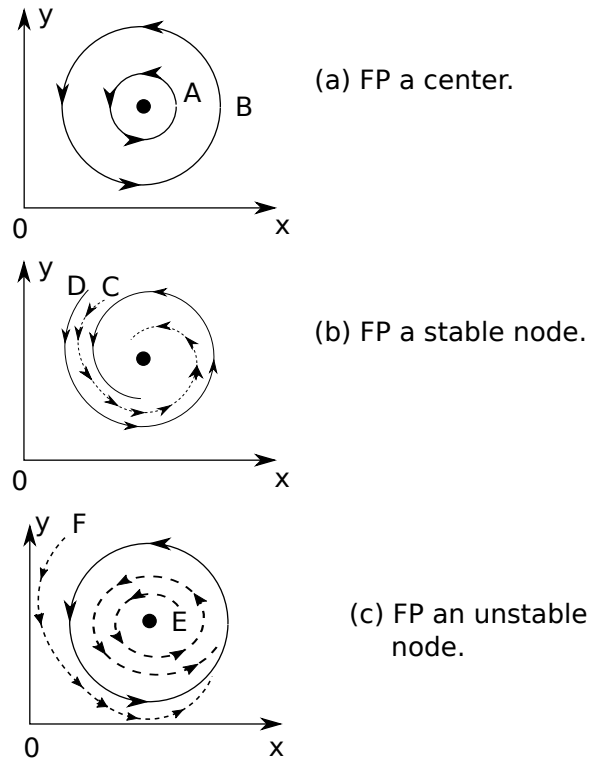


Figure 2: The heavy dot is the fixed-point (FP), located at (x^*, y^*) . As indicated, there are three possibilities for the stability of the FP. In 2.c the continuous, closed curve is a limit-cycle.

Figure 2-b, shows the situation for the co-existence state being a stable node. For this case all trajectories spiral into the F-P (x^*, y^*) .

The third case is the most interesting; see Figure 2-c. This illustrates that an unstable node may be surrounded by a stable limit-cycle [4, 5, 6, 7, 8], and all initial conditions give rise to trajectories approaching the limit-cycle. The maximum and minimum population values for both predator and prey, along with the period are determined by the parameters and not the initial conditions.

4 Effects of Culling the Predator

Culling of the predator, at time t_0 , is equivalent to changing the phase-plane point $(x(t_0), y(t_0))$ to $(x(t_0), y(t_0) - y_c)$, where $y_c > 0$ is the magnitude of

the cull. Note that in Figures 3 and 4, the “1” denotes the location of the trajectory at time t_0 , i.e., $(x(t_0), y(t_0))$, while “2” is the phase-space position after culling has taken place, i.e., $(x(t_0), y(t_0) - y_c)$.

Figure 3 illustrates the fact that if the FP is a stable node, the result of culling is that the system returns to the FP. In other words, culling does not change the long term behavior of the predator-prey system.

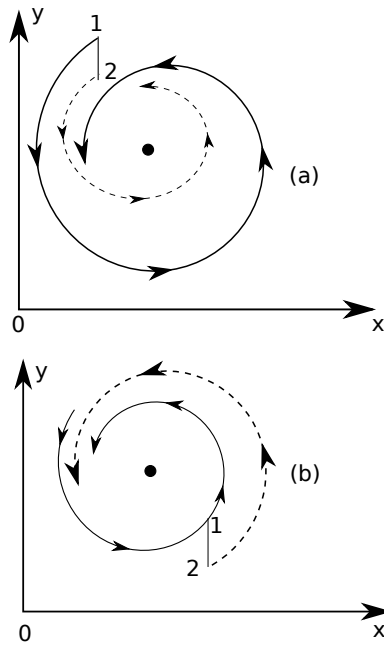


Figure 3: The FP, (x^*, y^*) , is a stable node.

Figure 4 shows the consequences of culling the predator for the case where the FP is an unstable node and it is surrounded by a stable limit-cycle. Again, the long time dynamics returns both the predator and prey populations to the original limit-cycle.

5 Summary

The general conclusion is that the standard deterministic ODE based models for a single predator and a single prey predict that culling of the predator will not have any long term effects on the predator/prey populations. Thus, to the degree that actual data may give the opposite result, it follows that for this situation, other types of mathematical models are required. One

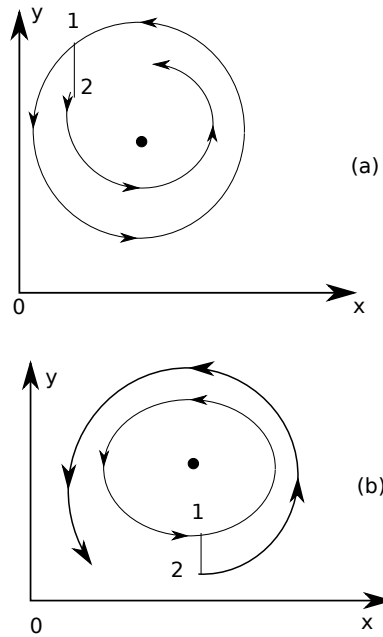


Figure 4: The FP, (x^*, y^*) is an unstable node, inside a stable limit-cycle.

possibility is the consideration of models which include stochastic effects [1, 5].

Acknowledgement

This work is an expansion of the discussion given in an e-letter to SCIENCE, which comments on the article by Goldfarb [2]. This e-letter can be found at <http://science.sciencemag.org/content/353/6304/1080.e-letters>.

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