

BEHAVIOURAL SENSITIVITY OF THE LOTKA-VOLTERRA MODEL

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ABSTRACT

The classic model for a deterministic, continuous growth, one-predator-one-prey system is that of Lotka and Volterra. It is well known that this model predicts neutral stability in which the constant amplitudes of the oscillations are determined by the initial conditions. Without changing the underlying model assumptions and by altering only the predator functional response to prey density, it is shown that damped oscillations towards stable equilibrium or explosive oscillations or a stable limit cycle can be generated as model output.

Introduction

The classic Lotka-Volterra model for a deterministic predator-prey system with continuous growth is the simplest representation of non-linear predator prey interaction. The model predicts oscillatory behaviour of the populations with constant amplitudes strongly dependent on the initial conditions. Thus the model predicts that an observed oscillation of many periods duration is due to an event that occurred earlier on, rather than being inherent to the system. In most texts the model is abandoned as it is felt that its unnatural behaviour makes further study unprofitable (Pielou 1977,p91¹). In order to obtain different behavioural modes the underlying basic model is then changed by assuming additional relationships amongst model variables- usually these comprise self regulating terms or a predator-prey response that takes into account the likely effect on per capita growth rates of the relative sizes of the interacting populations.

More realistic models resulting in damped oscillations towards stable equilibrium or explosive oscillations and eventual extinction of predator-prey populations or stable limit cycles are available in the literature (Leslie & Gower 1960, Freedman & Waltman 1975, Nicholson & Bailey 1935, Samuelson 1967²)

We show that the Lotka-Volterra model is behaviourally sensitive to the predator functional response to prey density and that all the behavioural modes mentioned above are possible for this model. We follow a system dynamics approach.

2. Freedman, H.I., and Waltman, P. (1975). Perturbation of two dimensional predator-prey equations. **SIAM J. Appl. Math.** 28, 1-10.

Leslie, P.H., and Gower, J.C. (1960). The properties of a stochastic model for the predator-prey type of interaction between two species. **Biometrika** 47, 219-234.

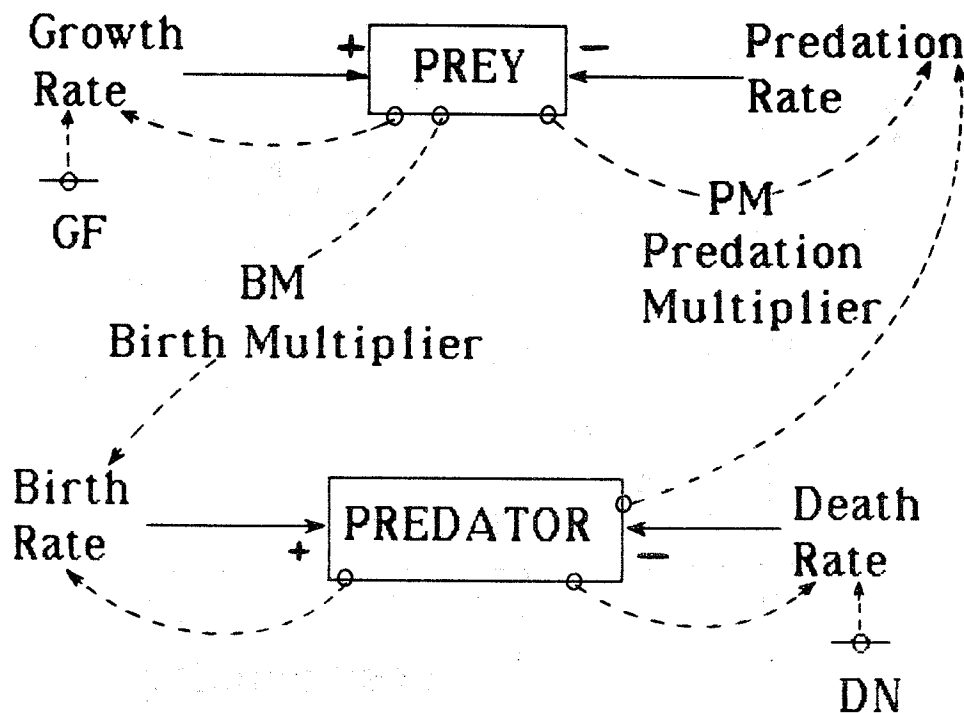
Nicholson, A.J., and Bailey, V.A. (1935). The balance of animal populations. **Proc. Zool. Soc. Lond.** 1935, 551-598.

Samuelson, P.A. (1967). A universal cycle? **Operations Research-Verfahren** 3, 307-320.

The Model

Consider a simple predator-prey model in which the following are assumed:

- (1) The prey has an unlimited food supply so the net prey growth rate is proportional to prey density;
- (2) The birth rate of the predator is proportional to predator density but is modified according to prey abundance;
- (3) The death rate of the predator is proportional to predator density;
- (4) The predation rate of prey is proportional to predator density and is modified according to prey density.



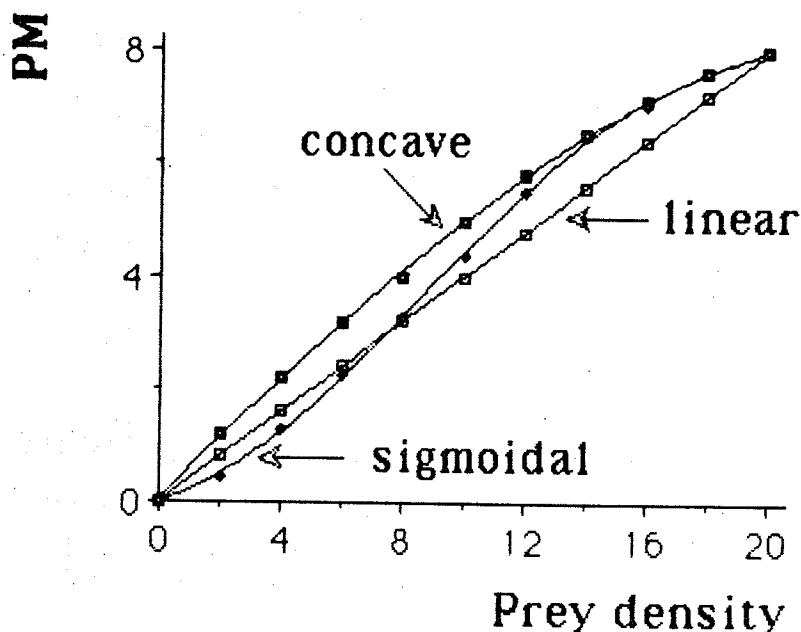
Model Formulation

$$\begin{aligned} d(\text{PRED})/dt &= \text{Birth Rate} - \text{Death Rate} \\ &= \text{PRED} * \text{BM}(\text{PREY}) - \text{PRED} * \text{DN} \end{aligned}$$

$$\begin{aligned} d(\text{PREY})/dt &= \text{Growth Rate} - \text{Predation Rate} \\ &= \text{PREY} * \text{GF} - \text{PRED} * \text{PM}(\text{PREY}) \end{aligned}$$

The functions BM and PM are increasing functions of PREY density - assume that BM varies between 0 and 0.4 and PM between 0 and 8 respectively, as PREY density increases from 0 to 20. BM is taken to be linear. Predator functional response graphs, PM, used in the model are shown below.

Predator Functional Responses



The Lotka-Volterra Model

BM and PM are both assumed linear.

$$\text{BM(PREY)} = (0.4/20) * \text{PREY}$$

$$\text{PM(PREY)} = (8/20) * \text{PREY}$$

yielding the following model equations:

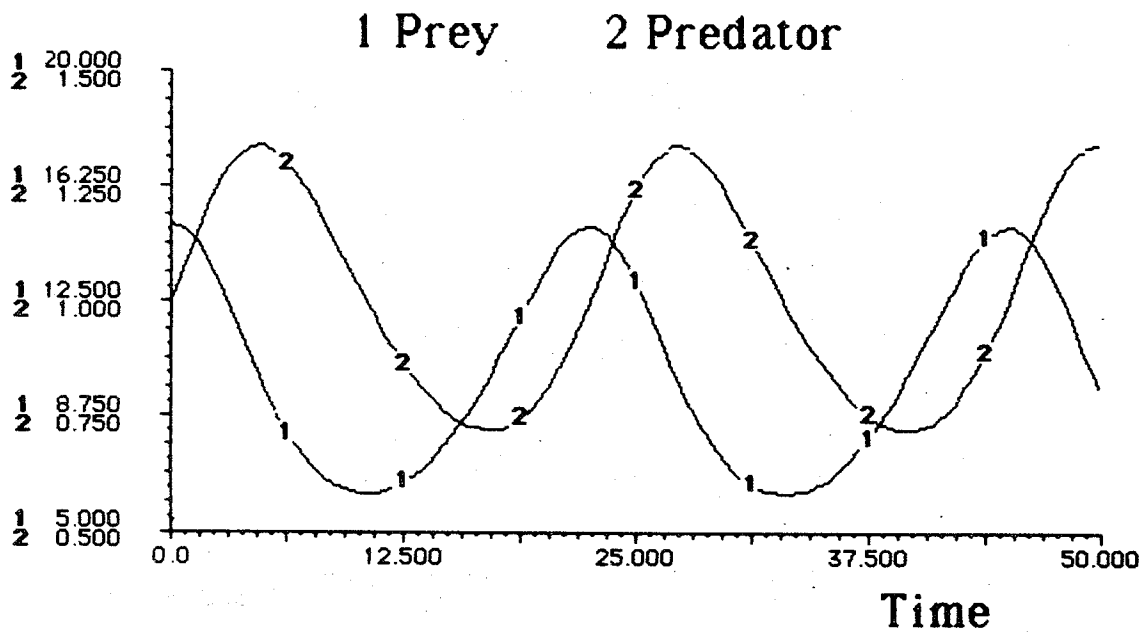
$$d(\text{PRED})/dt = \text{PRED} * (0.02 * \text{PREY} - \text{DN})$$

$$d(\text{PREY})/dt = \text{PREY} * (\text{GF} - 0.4 * \text{PRED})$$

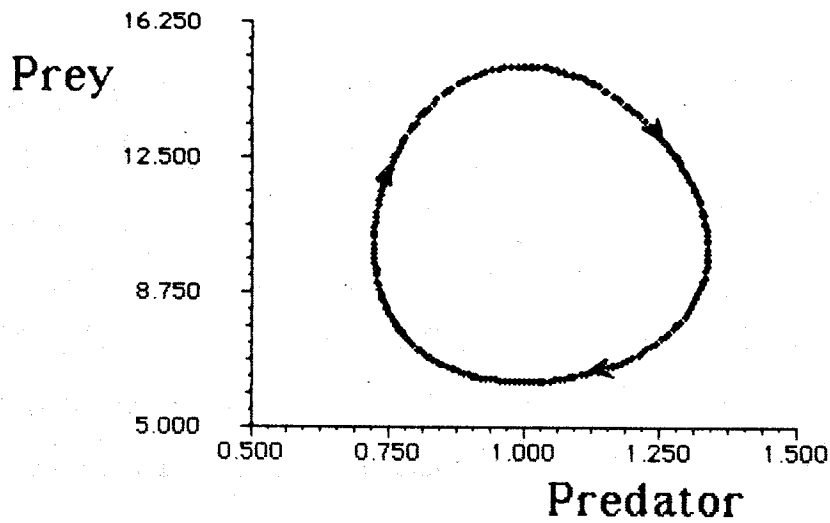
..... Lotka-Volterra equations

Both species oscillate periodically around their equilibrium values $\text{PRED} = \text{GF}/0.4$ and $\text{PREY} = \text{DN}/0.02$ with average population values equal to their equilibrium values. For $\text{GF} = 0.4$ and $\text{DN} = 0.2$ these values are respectively $\text{PRED} = 1$, $\text{PREY} = 10$. The constant amplitudes of the oscillations are determined by the initial values.

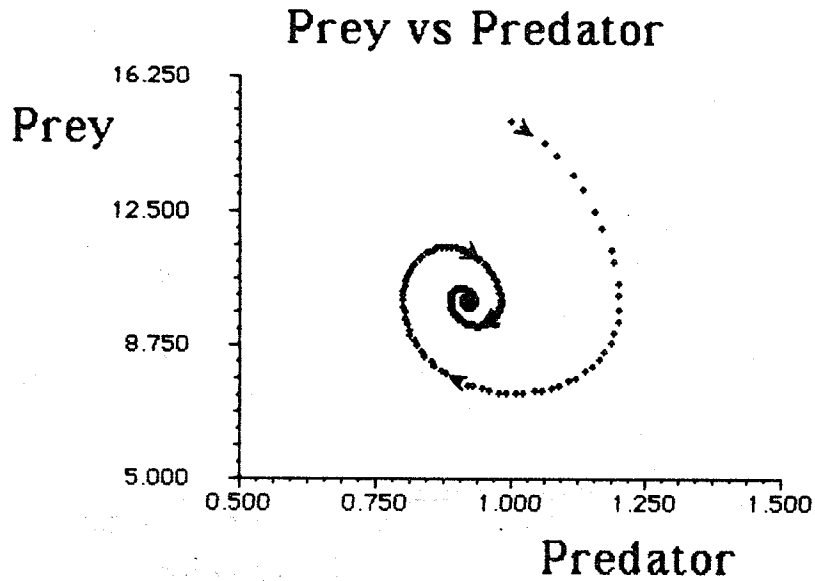
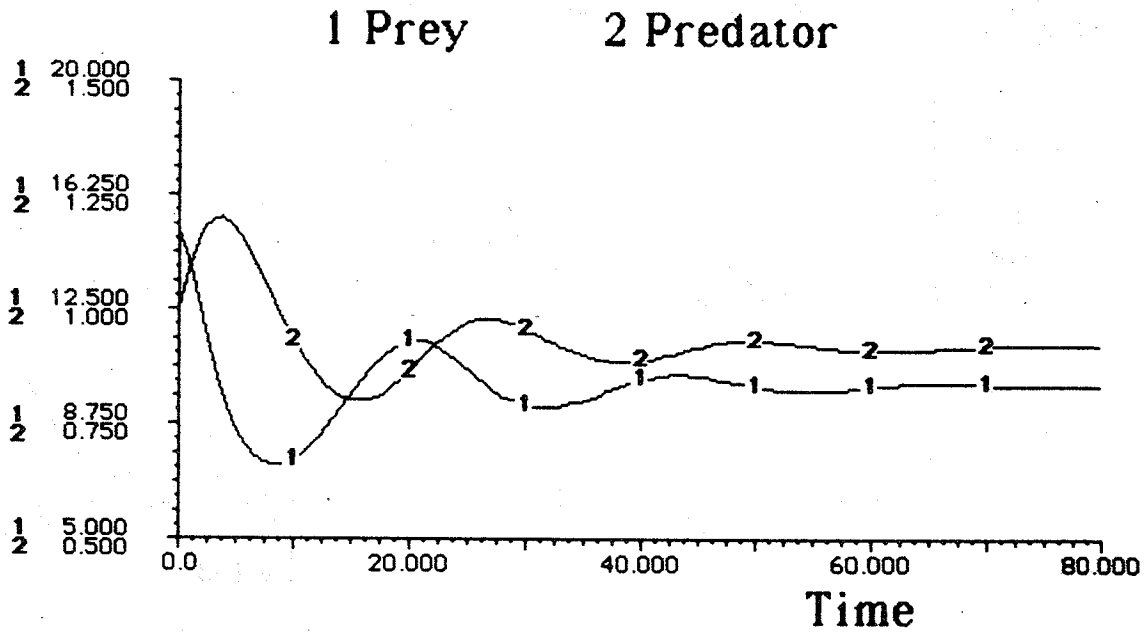
Predator linear response



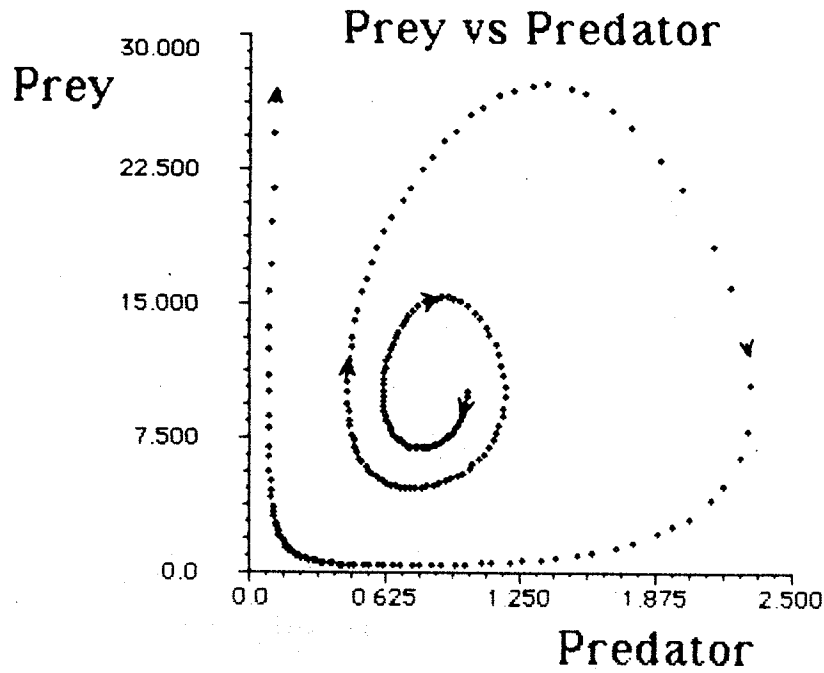
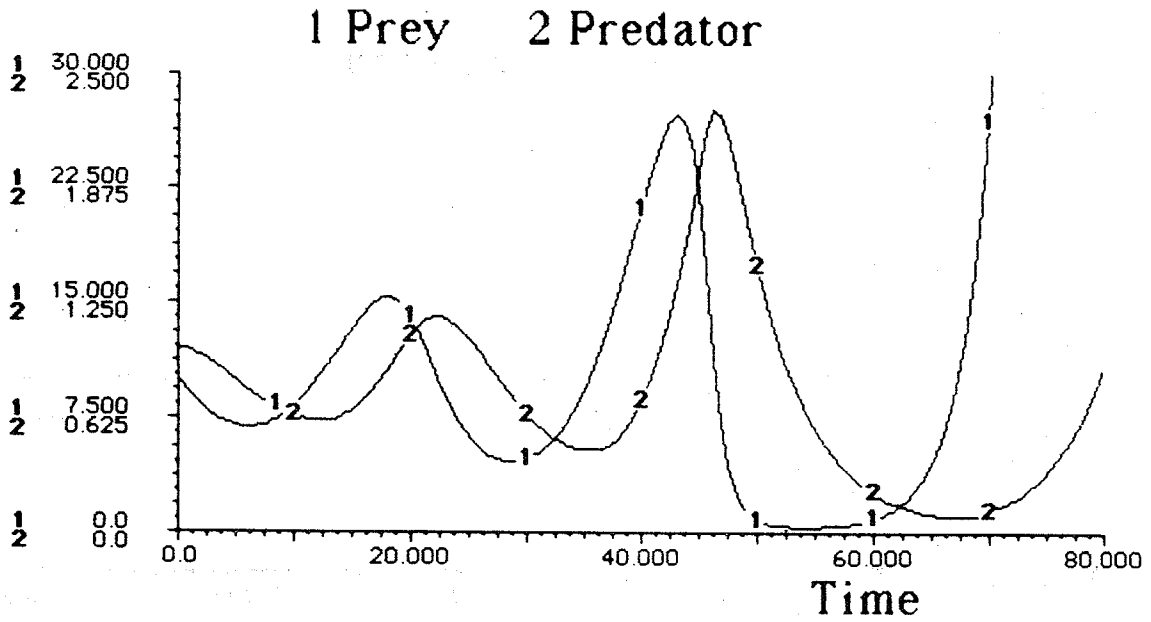
Prey vs Predator



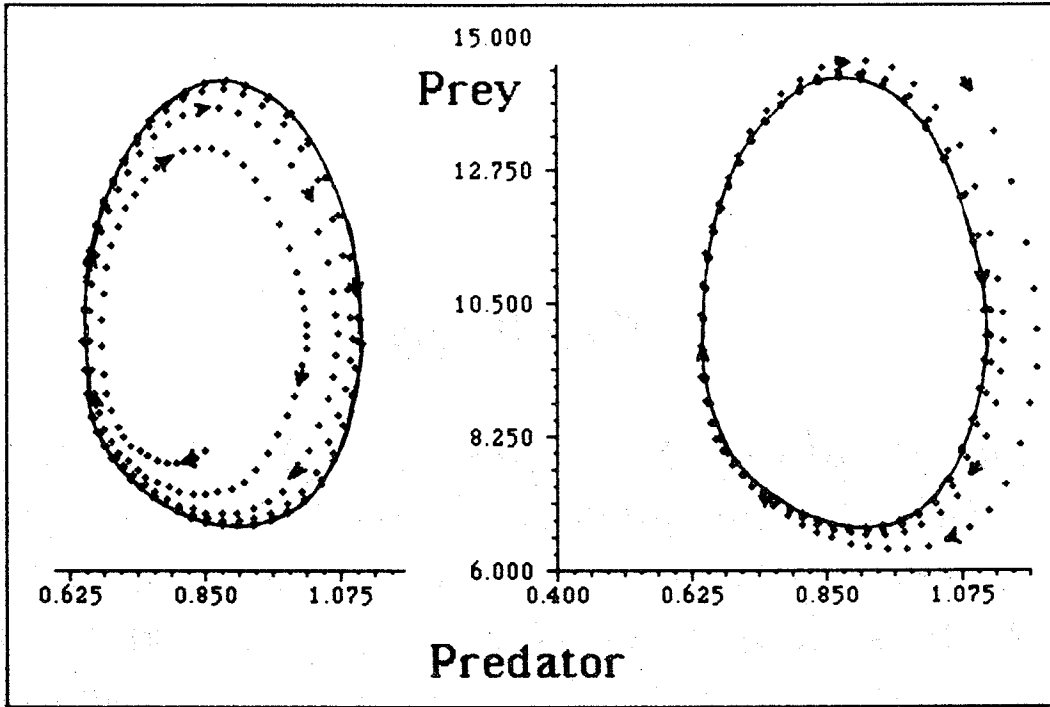
Predator sigmoidal response



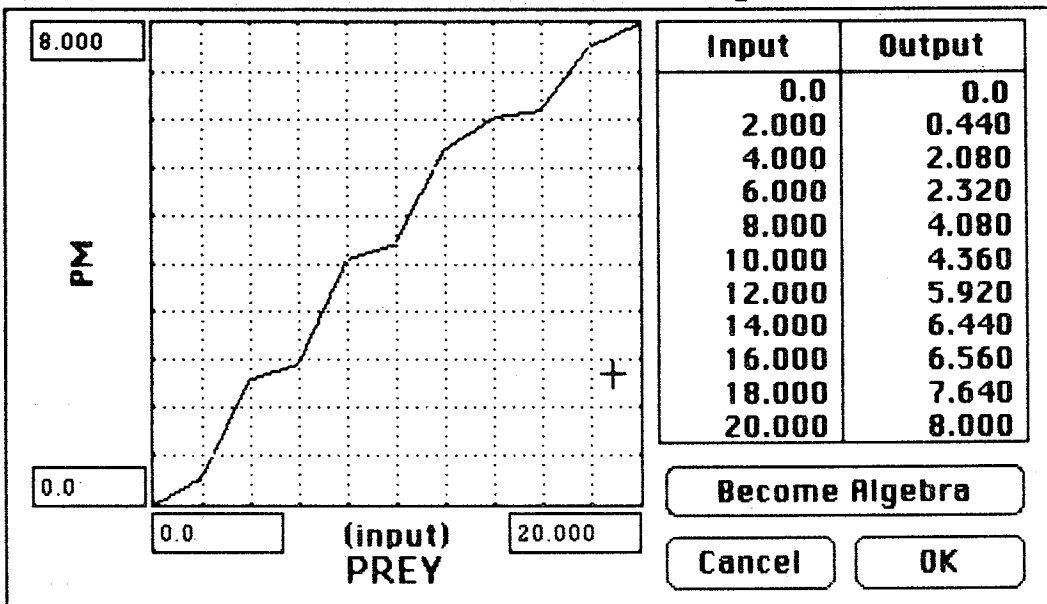
Predator concave response



Stable limit cycle



Predator functional response



Conclusion

The simple predator-prey model investigated here is behaviourally sensitive to the predator functional response to prey density. At least four distinct behavioural modes are possible- neutral stability, damped oscillations towards stable equilibrium, explosive oscillations and stable limit cycles.