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**Adaptive behaviour in a predator-prey model leads to multiple  
equilibrium states**

Alexander Pimenov<sup>1</sup>, Andrei Korobeinikov<sup>2,3</sup>,

Dmitrii Rachinskii<sup>4</sup>

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<sup>1</sup> Weierstrass Institute  
Mohrenstr. 39  
10117 Berlin, Germany  
E-Mail: alexander.pimenov@wias-berlin.de

<sup>2</sup> Centre de Recerca Matemàtica  
Campus de Bellaterra, Edifici C  
08193 Barcelona, Spain

<sup>3</sup> Departament de Matemàtiques  
Universitat Autònoma de Barcelona  
Campus de Bellaterra, Edifici C  
08193 Barcelona, Spain  
E-Mail: akorobeinikov@crm.cat  
Phone: +34 93 586 85 16

<sup>4</sup> Department of Mathematical Sciences  
The University of Texas at Dallas  
800 W. Campbell Road  
Richardson, Texas, USA

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Weierstraß-Institut für Angewandte Analysis und Stochastik (WIAS)  
Leibniz-Institut im Forschungsverbund Berlin e. V.  
Mohrenstraße 39  
10117 Berlin  
Germany

Fax: +49 30 20372-303  
E-Mail: [preprint@wias-berlin.de](mailto:preprint@wias-berlin.de)  
World Wide Web: <http://www.wias-berlin.de/>

## Abstract

There is evidence that multiple stable equilibrium states are possible in real-life ecological systems. In order to verify a hypothesis that such a multitude of equilibrium states can be caused by adapting of animal behaviour to changes of environmental conditions, we consider a simple predator-prey model where prey changes a mode of behaviour in response to the pressure of predation. This model exhibits two stable coexisting equilibrium states with basins of attraction separated by a separatrix of a saddle point.

## 1 Introduction

Predator-prey models in mathematical ecology typically have a single stable co-existing equilibrium state [1]. In some cases such models can also have a single stable limit cycle around an unstable equilibrium state; for instance, for some form of predation rate (such as Holling's type II functional response) this situation arises as a result of the so-called "effect of enrichment". Predator-prey models exhibiting the bistability or multistability are rather exotic in mathematical ecology; while a formal formulation of a model exhibiting multiple equilibrium states is a reasonably straightforward task, sensible biological or ecological justifications for such a model are usually dubious. The Allee effect, which is defined as a reduction of individual fitness at low population size, usually results in bistability, and a typical model with the Allee effect has two stable equilibrium states with basins of attraction divided by a stable separatrix of a saddle point located between them. However, in one of these stable equilibrium states the population size of the species exhibiting the Allee effect is equal to zero, and hence for such a biosystem the coexistence is only possible at a single stable equilibrium state as well.

On the other hand, there is evidence that multiple stable equilibria are possible and actually occur in both marine and terrestrial real life ecological systems. The most notorious example of the bi-stability is the so-called "deer crush" at Fort Rucker in Alabama, where an abundant deer population was reduced below a certain level by hunting, and now remains apparently stable at a very low level controlled by predators. While this scenario, known as "predator pit", is well described and it is understood that coyotes predating on fawn are responsible [2–6], to the best authors' knowledge, no sensible mathematical model exhibiting this type of dynamics was so far suggested.

We suggest that multiple stable coexisting equilibrium states can appear as a result of adaptation of the animal behaviour to environmental conditions. To illustrate this possibility, in this notice we introduce and consider a straightforward extension of the classic Lotka-Volterra predator-prey model, where the prey is assumed to be able to adapt the behaviour to the pressure of predation. This simple model confirms that even a very simple adoptive response can lead to the dynamics where a multitude of equilibrium states is possible.

## 2 Model

To illustrate the idea that adapting the behavior to changing environmental conditions can lead to a multitude of equilibrium states, we consider the classic Lotka-Volterra predator-prey model

$$\dot{u} = bu(1 - u/K) - auv, \quad \dot{v} = euv - dv. \quad (1)$$

Here  $u(t)$  and  $v(t)$  are sizes of the prey and the predator populations, respectively;  $b$  is per capita reproduction rate of the prey,  $K$  is the carrying capacity of environment, and  $d$  is per capita mortality rate of the predator in the absence of the prey;  $auv$  is attack rate, and  $e = \kappa a$ , where  $\kappa$  is the consumption efficiency. Let us now assume, that in this model, in response to an external challenge, individual prey animals can change their behavior choosing either risky or safe mode of behavior. In the risky mode the animal is more vulnerable to predation, while the carrying capacity (e.g., food availability) is larger (and hence the intraspecific competition is smaller); that is,  $a_R > a_S$  and  $K_R > K_S$  hold. For the consistency of the model, we also assume that safe behavior can imply a lower reproduction rate, that is  $b_R \geq b_S$  holds as well. (Here and further the subindexes  $S$  and  $R$  correspond to Safe and Risky behavior, respectively.)

This assumption agrees with the concept of the security cost: in this way, each of these two modes can be only relatively beneficial, and neither of these gives an absolute advantage. In general, we assume that a switch of the behavior occurs to maximize a relative Darwinian fitness. That is, if the pressure of intraspecific competition is higher than that of predation, then prey animals can prefer the risky mode, whereas if intraspecific competition is lower than the predation, then the animals can choose the safe mode. However, one hardly can expect that an individual animal is able to work out the optimal strategy, and hence it is reasonable to suppose that the switching strategy is non-ideal. Moreover, it is reasonable to assume that the levels of danger which individual animals are ready to tolerate, and hence individual switching thresholds, vary within a population and even within a herd.

For simplicity, we assume that the switching occurs instantly; that is each animal is either in the risky, or in the safe mode. Denoting  $u_R(t)$  and  $u_S(t)$  the subpopulations of  $u(t)$  which are in the risky and safe mode, and  $P_R$  and  $P_S$  the fraction of these, respectively, we obtain the following equations:

$$\begin{aligned} \dot{u}_R &= b_R u_R - c_R u_R^2 - h_R u_R u_S - a_R u_R v, \\ \dot{u}_S &= b_S u_S - c_S u_S^2 - h_S u_R u_S - a_S u_S v. \end{aligned}$$

Here  $c_i = b_i/K_i$ , and  $h_R$  and  $h_S$  are magnitudes of the inter-mode competition.

Taking into consideration that  $u(t) = u_R(t) + u_S(t)$  and  $P_R(t) + P_S(t) = 1$ , we obtain equations

$$\dot{u} = (b_S P_S + b_R(1 - P_S))u - (a_S P_S + a_R(1 - P_S))vu - (c_S P_S^2 + c_R(1 - P_S)^2 - (h_R + h_S)P_S(1 - P_S))u^2, \quad (2)$$

$$\dot{v} = (e_S P_S + e_R(1 - P_S))vu - dv. \quad (3)$$

To close this system, we have to define the function  $P_S$ . For the sake of simplicity, we assume that the switch of behavior occurs in response to the pressure of predation. Specifically, we

assume that  $P_S$  is a non-decreasing function of the probability for an animal to be killed by a predator. For the bilinear predation rate which corresponds to the law of mass action, this implies that  $P_S$  is a non-decreasing function of the predator population  $v(t)$ . For simplicity we assume that  $P_S$  depends on  $v$  linearly, that is

$$P_S = \min(\xi v, 1) \quad (4)$$

(see Fig. 1a). However, any other non-decreasing functions, such as a Michaelis-Menten response (Fig. 1b), or a sigmoidal function (Fig. 1c) can be used as well. Moreover, we have to stress that a specific form of this functional response does not affect the results and conclusions.

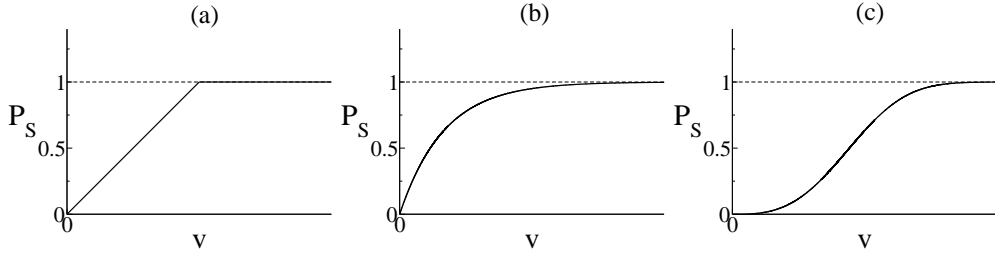


Figure 1: Possible forms of functional responses  $P_S(v)$ ; response  $P_S = \min(\xi v, 1)$  used in the paper, Michaelis-Menten response and a sigmoidal response.

### 3 Model properties

Similarly to the Lotka-Volterra predator-prey model (1), model (2), (3) always has a trivial equilibrium state  $E_{00}$ , where  $u = v = 0$ , and a predator-free equilibrium state  $E_{K0}$ , where  $u = K_R = b_R/c_R$  and  $v = 0$ . It is easy to see that the trivial equilibrium state is always a saddle point, whereas the type of point  $E_{K0}$  depends on the value of the basic reproduction ratio of the predator  $R_0 = e_R K_R/d$ . Specifically, if  $R_0 < 1$  then equilibrium state  $E_{K0}$  is a node and is globally asymptotically stable; the global stability implies that the model has no equilibrium states in the positive quadrant of the phase space, and that any solution initiated in this quadrant eventually converges to the equilibrium state. If  $R_0 > 1$  then equilibrium state  $E_{K0}$  is a saddle point. A saddle-node transcritical bifurcation occurs at point  $E_{K0}$  at  $R_0 = 1$ . (It can be mentioned that equilibrium state  $E_{K0}$  is globally asymptotically stable when  $R_0 = 1$  as well.) The global stability of point  $E_{K0}$  for all  $R_0 \leq 1$  can be proved using the direct Lyapunov method (e.g. see [1]). The proof of the saddle-node bifurcation involves the standard linear analysis. Both proofs are rather lengthy and technical, and we omit these; in any case, these two equilibrium states are the same as for the basic Lotka-Volterra model. The concept of the basic reproduction ratio is adapted from the mathematical epidemiology. The basic reproduction ratio has a transparent interpretation: it is equal to an average number of offsprings produced by a single predator introduced into a predator-free environment during its entire life.

Apart from these two equilibrium states which always exist, for all  $R_0 > 1$  model (2), (3) has from one to three positive equilibrium states, and it is this multitude of equilibrium states that

makes it different from the basic model (1). Indeed, at a positive equilibrium state, the equalities

$$(b_S P_S + b_R(1 - P_S)) - (a_S P_S + a_R(1 - P_S))v - (c_S P_S^2 + c_R(1 - P_S)^2 - (h_R + h_S)P_S(1 - P_S))u = 0, \quad (5)$$

$$(e_S P_S + e_R(1 - P_S))u - d = 0 \quad (6)$$

hold. Equality (6) implies

$$u = \frac{d}{e_S P_S + e_R(1 - P_S)}. \quad (7)$$

Substituting (7) into (5), we obtain

$$\begin{aligned} c_R d(R_0 - 1) + (\kappa(b_S a_R - 2b_R a_R + b_R a_S) + d(2c_R + h_R + h_S))P_S \\ + (\kappa(b_S - b_R)(a_S - a_R) - d(c_S + c_R + h_R + h_S))P_S^2 \\ - \kappa a_R^2 v - \kappa(a_R^2(a_S - a_R)^2)P_S v - \kappa(a_S - a_R)^2 P_S^2 v = 0. \end{aligned} \quad (8)$$

For  $P_S$  defined by (4), this equation is a polynomial of the third order, and hence it has one to three real roots; each of these roots corresponds to an equilibrium state. Figures 2 (a) to (f) show null curves  $\dot{u} = 0$  and  $\dot{v} = 0$ , defined by equalities (5) and (6), in the phase space for  $R_0 = 0.5, 10.0, 16.7, 25.0, 50.0, 100.0$ , respectively. Intersections of the null curves correspond to the equilibrium states.

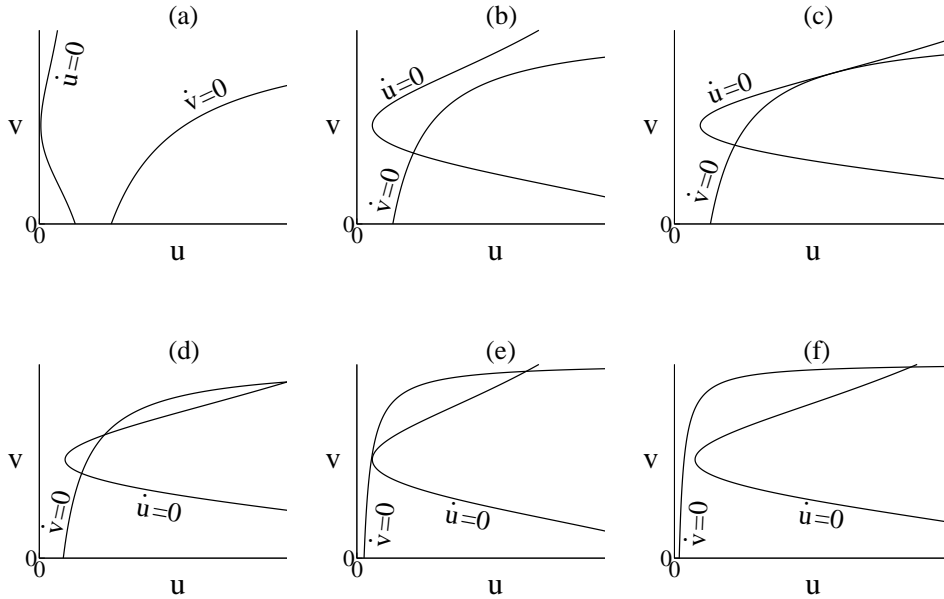


Figure 2: Null curves  $\dot{u} = 0$  and  $\dot{v} = 0$ , defined by (5) and (6), in the phase space. In these Figures,  $R_0$  is equal to 0.5, 10.0, 16.7, 25.0, 50.0, 100.0, respectively.

These Figures, and in particular Figures 2 (c) and (e), show that the second and third equilibrium states appear and disappear as a result of a fold (saddle-node) bifurcation, which occurs when two null-curves have a common tangent line. The standard linear analysis in the vicinity of the equilibrium states yields that when three equilibrium states exist then the middle point is always a saddle point, whereas the upper and lower points are stable nodes or foci. Figures 3

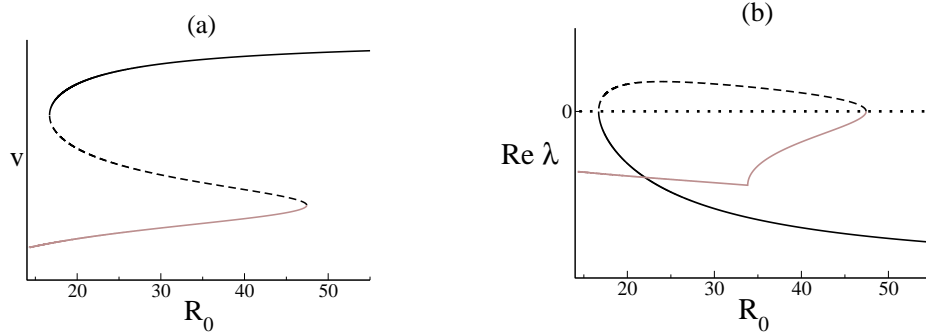


Figure 3: Bifurcation diagrams for the fixed points of system (2), (3). Fig. (a) shows equilibrium levels of  $v$  for varying predator's basic reproduction number  $R_0$ ; in this figure, the top branch (solid line) and the bottom branch (grey solid line) are stable points (nodes or foci), whereas the middle branch (a dashed line) is a saddle. Fig. (b) shows maximal values of the real parts for the eigenvalues of the linearized system for the corresponding branches. The data are obtained for  $b = d = \kappa = \xi = 1$ .

(a) and (b) show the corresponding bifurcation diagrams, which are obtained numerically. The corresponding phase portrait of the system with three positive equilibrium states is given in Figure 4. In this Figure, both stable equilibrium states are nodes; please note that one or both stable points can also be foci.

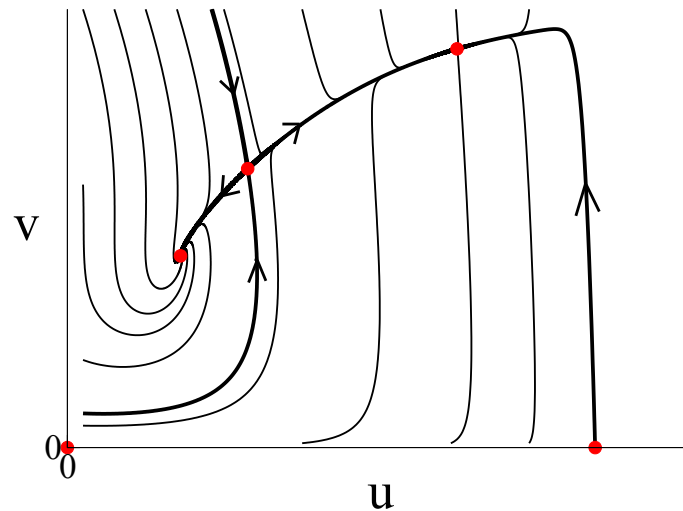


Figure 4: Schematic phase portrait of system (2), (3) when it has three positive equilibrium states.

For other reasonable non-linear types of functional response  $P_S(v)$ , such as these in Fig. 1, the outcome will be qualitatively the same.

## 4 Conclusion

The objective of this notice was to demonstrate that the ability to adapt the behaviour to varying environmental conditions can lead to the existence of multiple equilibrium states that were observed in real life ecosystems. In order to illustrate this concept, we considered a simple and straightforward extension of the Lotka-Volterra predator-prey model, where the prey is assumed to be able to change the mode of behaviour in response to a level of danger from the predator (that is to the probability for an individual animal to be attacked by a predator). The straightforward analysis shows that this hypothesis leads to a model which may have two stable positive equilibrium states separated by an unstable equilibrium.

The model postulates that the secure behaviour inflicts a certain cost. For an animal population, it is natural to associate the cost with a reduction of the reproduction rate or an increase of the intraspecific competition (and hence a reduction of the reproduction rate too). Consequently, we only consider the adaptive changes of behaviour which increase a relative Darwinian fitness rather than gain an absolute advantage. In other words, we assumed that the objective of a change of behaviour is to increase the current Darwinian fitness, and hence, for instance, in the framework of the Lotka-Volterra model the prey should consider both the pressure of predation and that of the intraspecific competition, choosing a strategy which maximises the fitness with respect to both these factors.

For the sake of simplicity, in this notice we considered only the simplest possibility, and only one response and one adaptation mechanism, namely the response to the pressure of predation leaving out of the consideration a possibility to respond to other challenges, such as limited resources and intraspecific competition. Furthermore, we disregarded a possibility for the predator to adapt its behaviour. Both these factors can be included into a model, but the principal conclusion would be the same, namely the existence, for some parameters, of multiple stable equilibrium states.

For this particular model, a multitude of equilibrium states arises due to the fact that the ability to adapt the behaviour implies to some extent is equivalent to a rate of predation which does not monotonously grow with the abundance of the predator. In contrast, for this model the change of the prey behaviour implies that an increment of the predator can result in the decrease of the attack rate. Such a non-monotonicity of the attack rate leads to multiple equilibrium states. In some aspects, these effects and the model itself are not dissimilar to models considered in [7, 8], where the impact of a short-term refuge for the prey was studied.

Also, we have to note that the idea of adapting the prey behaviour to the predation pressure leads to a model with a “non-symmetric predation”, where the decrease of the prey population caused by predation is not proportional to the increase of the predator population itself, as it is in the original Lotka-Volterra model. Some properties of models with the non-symmetric predation were considered in [9] where sufficient conditions for their global stability were found.



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