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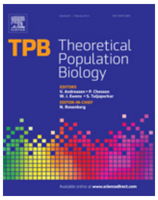

Adaptive behaviour and multiple equilibrium states in a predator–prey model

Alexander Pimenov[a], Thomas C. Kelly[b], Andrei Korobeinikov[c,d], Michael J.A. O'Callaghan[e], Dmitrii Rachinskii[f,*]

[a] *Weierstrass Institute, Mohrenstrasse 39, D-10117 Berlin, Germany*
[b] *Department of Biology, Earth and Environmental Science, University College Cork, Ireland*
[c] *Centre de Recerca Matemática, Campus de Bellaterra, Edifici C, 08193 Barcelona, Spain*
[d] *Departament de Matemàtiques, Universitat Autònoma de Barcelona, Campus de Bellaterra, Edifici C, 08193 Barcelona, Spain*
[e] *Department of Applied Mathematics, University College Cork, Ireland*
[f] *Department of Mathematical Sciences, The University of Texas at Dallas, 800 W. Campbell Road, Richardson, TX 75080, USA*

HIGHLIGHTS

- There are evidences that multiple stable equilibria are possible in ecosystems.
- We suggest that multiple equilibria can arise as a result of adaptive behaviour.
- We construct a simple mathematical model, which illustrate this hypothesis.
- The model is a straightforward extension of the classical Lotka–Volterra model.

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ABSTRACT

There is evidence that multiple stable equilibrium states are possible in real-life ecological systems. Phenomenological mathematical models which exhibit such properties can be constructed rather straightforwardly. For instance, for a predator–prey system this result can be achieved through the use of non-monotonic functional response for the predator. However, while formal formulation of such a model is not a problem, the biological justification for such functional responses and models is usually inconclusive.

In this note, we explore a conjecture that a multitude of equilibrium states can be caused by an adaptation of animal behaviour to changes of environmental conditions. In order to verify this hypothesis, we consider a simple predator–prey model, which is a straightforward extension of the classic Lotka–Volterra predator–prey model. In this model, we made an intuitively transparent assumption that the prey can change a mode of behaviour in response to the pressure of predation, choosing either "safe" of "risky" (or "business as usual") behaviour. In order to avoid a situation where one of the modes gives an absolute advantage, we introduce the concept of the "cost of a policy" into the model. A simple conceptual two-dimensional predator–prey model, which is minimal with this property, and is not relying on odd functional responses, higher dimensionality or behaviour change for the predator, exhibits two stable co-existing equilibrium states with basins of attraction separated by a separatrix of a saddle point.

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1. Introduction

Predator–prey models in mathematical ecology typically have a single stable equilibrium state (e.g. Korobeinikov, 2009). 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"

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[*] Corresponding author.
E-mail addresses: alexander.pimenov@wias-berlin.de (A. Pimenov), t.kelly@ucc.ie (T.C. Kelly), akorobeinikov@crm.cat (A. Korobeinikov), mja.ocallaghan@ucc.ie (M.J.A. O'Callaghan), dmitry.rachinskiy@utdallas.edu (D. Rachinskii).

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(Berryman et al., 1995; Rosenzweig, 1971). Predator–prey models exhibiting the bi-stability or multi-stability are rather exotic in mathematical ecology. While a formal construction of a model exhibiting multiple equilibrium states is a reasonably straightforward task, realistic 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 bi-stability, 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 (Stephens et al., 1999; Stephens and Sutherland, 1999; Scheuring, 1999; Petrovskii et al., 2002). 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, co-existence 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 bi-stability is the so-called "deer crush" at Fort Rucker in Alabama (Jackson and Ditchkoff, 2013; McCoy et al., 2013), 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 (Jackson and Ditchkoff, 2013; McCoy et al., 2013; Kilgo et al., 2010, 2012), to the authors' best knowledge, no entirely satisfactory mathematical model based on transparent and biologically sound hypotheses and exhibiting this type of dynamics has been so far investigated. (The "predator pit" scenario is not uncommon and was observed in variety of other ecosystems; see e.g. Smout et al., 2010.) Moreover, it is understood that a multitude of co-existing equilibrium states can be formally achieved with the use of non-monotonic functional responses for the predator. Thus, a non-monotonic with respect to the prey attack rate can lead to this outcome. However, while a number of such functional responses was suggested, to the best authors' knowledge, the use of neither of these was so far sufficiently biologically motivated. (We have to stress that here we are discussing the total rather than per capita functional responses, as non-monotonicity of the per capita responses is reasonably common.)

We suggest that multiple stable co-existing 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 adaptive response can lead to the dynamics where a multitude of co-existing equilibrium states is possible.

2. Model

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

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

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 κ is the consumption efficiency.

Let us now assume that, in response to an external challenge, individual prey animals can change their behaviour choosing either *risky* or *safe* mode. In the risky mode of behaviour 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. (Here and further the subscripts S and R correspond to *Safe* and *Risky* behaviour, respectively.) For consistency, we also assume that safe behaviour can imply a lower reproduction rate, that is $b_R \geq b_S$ holds as well. These assumptions are in agreement with the idea that security should be paid for (e.g., Chiorino et al., 1999; Ruxton, 1995): in this way, neither of these two modes gives an absolute advantage, and each of these is only relatively beneficial. For instance, in a non-homogeneous environment the prey in the safe mode avoids the patches where predator's attack is more likely to occur (e.g., concealed approach of a predator is possible), thus sacrificing the resource of these patches. Another example is herding: a large herd gives more protection for the cost of more confined access for its individual members to resources (food). A reduction of the reproduction rate b in the safe mode may be caused by a low food supply or avoiding richer but more dangerous breeding grounds.

For simplicity, we assume that the modes switch instantly, and hence 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 modes, and $P_R(t)$ and $P_S(t)$ the fractions of these, respectively, we obtain the following equations:

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

Here $c_i = b_i/K_i$, and h_R and h_S are magnitudes of the inter-mode competition. Since $K_R > K_S$ and $b_R \geq b_S$, $c_R < c_S$ holds. Taking into consideration that $u(t) = u_R(t) + u_S(t)$ and $P_R(t) + P_S(t) = 1$, and hence $u_S = P_S u$ and $u_R = (1 - P_S)u$, we obtain equations

$$\begin{aligned} \dot{u} \;=\; & (b_S P_S + b_R(1 - P_S))u - (a_S P_S + a_R(1 - P_S))vu \\ & - (c_S P_S^2 + c_R(1 - P_S)^2 + (h_R + h_S)P_S(1 - P_S))u^2, \end{aligned} \tag{2}$$

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

Condition

$$h_S + h_R - 2c_R \geq 0 \tag{4}$$

is necessary to avoid biologically infeasible equilibrium states. This condition implies that prey in both modes is exploiting the same environment and utilizing (with different efficiency) the same resources. This principally differs from the concepts of multiple patches environment, or a refuge, when the prey in a patch (or in the refuge) is assumed to have no access to resource in other patches, and hence all $h_{i,j} = 0$.

To close this system, we have to define the function $P_S(t)$. It appears to be reasonable to assume that a switch of the behaviour occurs to maximize a relative Darwinian fitness. That is, if the pressure of intraspecific competition is higher than that of predation, the prey can prefer to accept a higher level of the risk of predator attack to get access to additional resources, whereas when the pressure of intraspecific competition is lower than that of predation, then the animals can choose the safe mode. However, we hardly can expect that an individual animal would be able to work out the optimal strategy aimed at optimizing of the fitness, and hence it is reasonable to suppose that an individual switching strategy is non-ideal. Moreover, it is reasonable to assume that the levels of the pressure, which individual animals are ready to tolerate, and hence their individual switching thresholds, vary within a population and even within a herd. Hence we have to assume that the thresholds are distributed in the population, and the distribution $\rho(A)$ is a function of the pressure $A(t)$. The relationship of functions $\rho(A)$ and $P_S(A)$ is obvious: it is easy to see that

$$P_S(A) = \int_0^A \rho(\tau)\, d\tau,$$

and that $\rho(A) = \frac{dP_S}{dA}$.

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