PIGS STEALING AND WOLFED DOWN PIGLETS: THE INFLUENCE OF KLEPTOPARASITISM ON A SIMPLE TROPHIC NETWORK

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Abstract
In ecological models complexity often arises due to the presence of interactions complicating the trophic network. An example of this it is the case of kleptoparasitism: a herbivorous scavenger *B* competes with the predator *W* for carcasses of its prey *D*. *B* may also be preyed on by *W*, in its juvenile age, and it competes with *D* for vegetation. This scenario is inspired by the behavior of wild boar observed in the Northern Apennine, Italy, competing with wolves for carcasses of fallow deer. The dynamical system presented here is a version of a model already studied by the authors, simplified in order to single out the essence of kleptoparasitism as an interaction giving rise to complexity.

Key words
Trophic webs, scavenging, bifurcation analysis.

1 Introduction

Studying the quantitative evolution of populations in ecosystems is a well developed branch of mathematical ecology, that dates back to the first models of Lotka and Volterra.

Traditionally, the problem of time variability of the abundance of two or more species in a given environment is treated by studying a system of coupled differential equations, whose unknown functions quantify the amounts of the different species evolving with time. From a physical point of view, the most ambitious goal should be of being able to deduce those models from “first principles.

The analytical form of coupling reflects the type of interaction among species, as e.g. cooperation (the co-presence of two species increase growth rates), competition (the co-presence of two species is negative) or predation (the co-presence of two species influences negatively the prey and positively the predator). Here we consider an ecological system formed by an external resource, which is not included as dynamical variables, supporting the growth of two consumers, of population *D* and *B*. These two primary consumers are in competition with each other, so that a logistic dynamics is formulated for them, with the carrying capacity depending on the abundance of the other species’ population.

A predator of population *W* preys on those primary consumers; moreover, the consumer of population *B* is *a scavenger*, that consumes the carcasses of species *D* killed by *W*. This means that there is *prey sharing* between *B* and *W*, because only a fraction $\psi \in [0,1]$ of the carcasses will be actually consumed by *W*. This fraction may be either a fixed parameter, or a function of the populations *B* and *W*. The first case mimics a situation in which predators exhibit partial prey consumptions and leave a fraction $1-\psi$ of the carrions unconsumed. In the second case, the individuals of *B* and of *W* compete for the use of the carrions, hence the amount of preys successfully defended by *W* depends on the ratio $\frac{W}{B}$, and on some *relative strength* of the individuals of the two species. In the latter case, one speaks about *kleptoparasitism of B on W*.

In section 2 the system of the ODEs describing such ecosystem is described, both for fixed prey sharing and for kleptoparasitism. Then, the different scenarios are investigated via a bifurcation analysis as the strength of prey sharing (or kleptoparasitism) is varied. Conclusions and a sketch of future work are illustrated in section 3.

2 The system(s) of ODEs

The system of coupled, non linear ODEs of the ecosystem described above reads:

$$\begin{cases} \dot{D} = \alpha\left(1 - \dfrac{\beta D + \gamma B}{\alpha}\right)D + \\ -\rho DW, \\ \dot{B} = \omega\left(1 - \dfrac{\tau D + \vartheta B}{\omega}\right)B + \\ -\xi BW + \mu[1 - \psi(B,W)]DW, \\ \dot{W} = \eta\psi(B,W)DW + \\ +\nu BW - \delta W, \end{cases} \tag{1}$$

where the term $\psi(B,W)$, represents the fraction of preys consumed by W and may either be a constant

$$\psi(B,W) = 1 - \lambda \ \forall \ B,W, \tag{2}$$

or a function ranging from 0 to 1, and depending on the relative force of individuals of the B and W species:

$$\psi(B,W) = \frac{W}{W + \lambda B}. \tag{3}$$

In both (2) and in (3) prey sharing grows with λ.
Before discussing briefly the different scenarios arising for different levels of prey sharing we report the asymptotic equilibrium attained by the three species arrive *without prey sharing* at all, namely for $\lambda = 0$: in this case system (1) simply reduces to:

$$\begin{cases} \dot{D} = \alpha\left(1 - \dfrac{\beta D + \gamma B}{\alpha}\right)D - \rho DW, \\ \dot{B} = \omega\left(1 - \dfrac{\tau D + \vartheta B}{\omega}\right)B - \xi BW, \\ \dot{W} = \eta DW + \nu BW - \delta W. \end{cases}$$

Running the simulations for reasonable values of the other parameters, we obtain the following Figure 1, in which the three-dimensional phase space (D,B,W) is represented by two orthogonal planes:

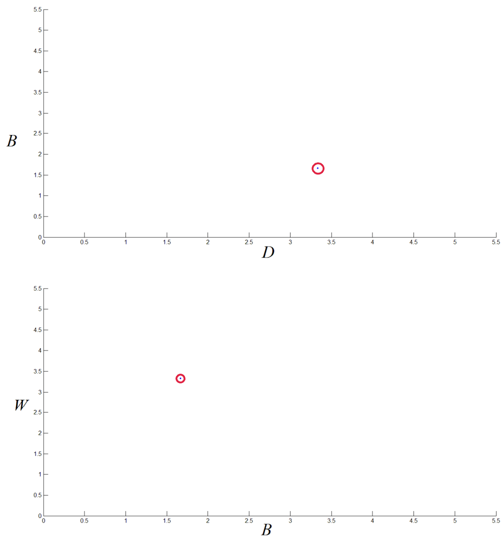


Figure 1. The asymptotic equilibrium in the scenario *without prey sharing*. Top panel: the B vs. D section of the phase space. Bottom panel, the W. vs. D section.

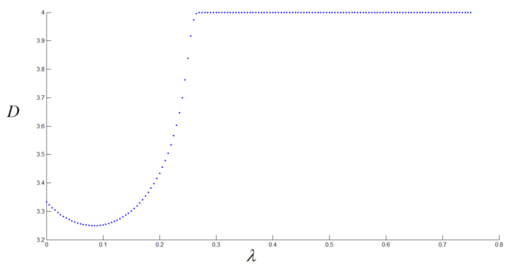
In the next sections 2.1 and 2.2 we study how this pattern changes by varying the low governing prey-sharing.

2.1 partial prey-cosumption

In this case, the system of ODEs reads:

$$\begin{cases} \dot{D} = \alpha\left(1 - \dfrac{\beta D + \gamma B}{\alpha}\right)D + \\ -\rho DW, \\ \dot{B} = \omega\left(1 - \dfrac{\tau D + \vartheta B}{\omega}\right)B + \\ -\xi BW + \mu\lambda DW, \\ \dot{W} = \eta(1 - \lambda)DW + \\ +\nu BW - \delta W, \end{cases}$$

The bifurcation diagrams of the system above are represented in the three panels of Figure 2, where the asymptotic value reached by the given species is reported as a function of λ.



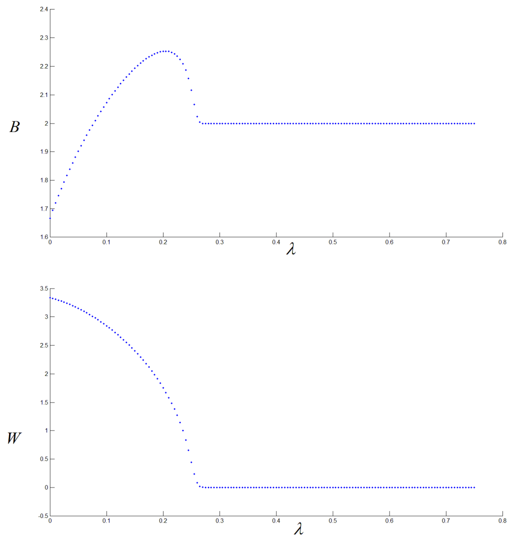


Figure 2. Bifurcation analysis of the system with partial prey consumption.

Looking at Figure 2, one learns that increasing the degree of prey sharing then the *B* takes an advantage, while *W* decreases. However, while for *W* the loss in monotonic, and W gets extinct in the correspondence of a critical value of prey-sharing, its concurrent *B* enjoys its maximum advantage *before* the predator gets extinct, because it cannot kill *D* by itself, and undergoes *D*'s concurrence more severely as *W* decreses.

2.2 Competition and kleptoparasitism

When proper competition exists between *B* and *W* for the carrions of *D*, the system (1) becomes:

$$\begin{cases} \dot{D} = \alpha\left(1 - \dfrac{\beta D + \gamma B}{\alpha}\right)D + \\ -\rho DW, \\ \dot{B} = \omega\left(1 - \dfrac{\tau D + \vartheta B}{\omega}\right)B + \\ -\xi BW + \mu\left(1 - \dfrac{W}{W + \lambda B}\right)DW, \\ \dot{W} = \dfrac{\eta DW^2}{W + \lambda B} + \nu BW - \delta W. \end{cases}$$

While all the other parameters stay fixed, this time one varies λ in the simulations of these ODEs, and obtains the scenarios reported in Figure 3.

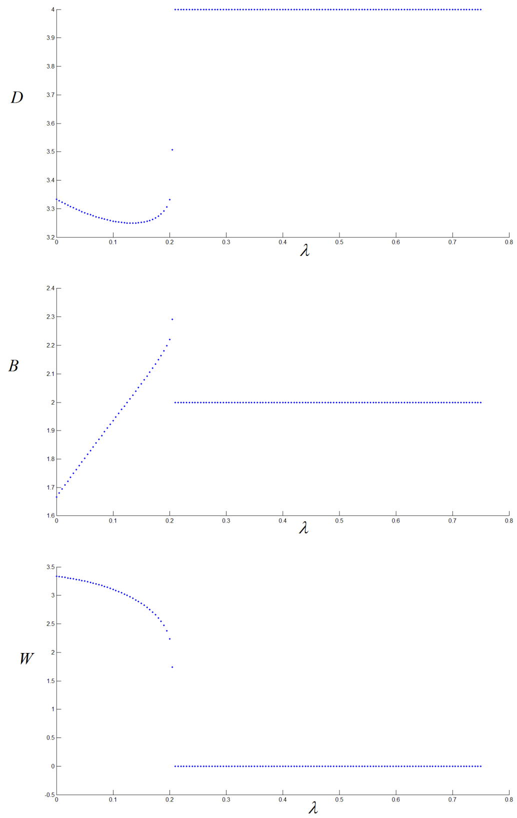


Figure 3.Bifurcation analysis of the system with competition between *B* and *W*.

As before *W* decreases monotonously until extinction. *D* first decreases with λ until a threshold λ_s=0.2, because increasingnumber of *B*, increases competition with *D* for the common resource. When *W* is much reduced however D starts to increase again. The big difference with respect to the case described in section 2.1 is that the transition to the final scenario, with $W = 0$, takes place *abruptly*, with some sort of very sudden phase transition.

3 Conclusion

The original design of the ODEs (1) was conceived to describe the trophic web formed by a common pool of vegetation, fallow deer and wild boar grazing it, and wolves preying of the two other mammals [Materassi, Berzi, Innocenti, Focardi, 2017]. Kleptoparasitism was described between wild boar and wolves.

In the original model, many more complications were present, namely: age structure for the wild boar population (only the youngster of which could be preyed on by wolves), specialization of preying by wolves (preying on the more abundant prey, whether fallow deer or piglets), vegetation as a proper dynamical variables.

Here many simplifications were introduced but still the effects are the same: exaggerating prey sharing, wolves get extinct while wild boar undergoes a competition with fallow deer that would have been lighter in the presence of wolves.

References

Materassi M., G. Innocenti, D. Berzi, S. Focardi, “Kleptoparasitism and complexity in a multi-trophic web”, Ecological Complexity 29 (2017) 49–60.