Oscillations from satiation of predators

M. N. Kuperman\textsuperscript{a,b,c}, M. F. Laguna\textsuperscript{a,b}, G. Abramson\textsuperscript{a,b,c}, A. Monjeau\textsuperscript{a,d}, J. L. Lanata\textsuperscript{e}

\textsuperscript{a}Consejo Nacional de Investigaciones Científicas y Técnicas
\textsuperscript{b}Centro Atómico Bariloche (CNEA), R8402AGP Bariloche, Argentina
\textsuperscript{c}Instituto Balseiro, Universidad Nacional de Cuyo, Argentina
\textsuperscript{d}Fundación Bariloche, R8402AGP Bariloche, Argentina
\textsuperscript{e}Instituto de Investigaciones en Diversidad Cultural y Procesos de Cambio, CONICET-UNRN, R8400AHL Bariloche, Argentina

Abstract

We develop a mathematical model of extinction and coexistence in a generic predator-prey ecosystem composed of two herbivores in asymmetrical competition and a hunter exerting a predatory pressure on both species. With the aim of representing the satiety of hunters when preys are overabundant, we introduce for the predation behavior a dependence on preys density. Specifically, predation is modeled as growing proportionally to the presence of herbivores at low density, and saturating when the total population of prey is sufficiently large. The model predicts the existence of different regimes depending on the parameters considered: survival of a single species, coexistence of two species and extinction of the third one, and coexistence of the three species. But more interestingly, in some regions parameters space the solutions oscillate in time, both as a transient phenomena and as persistent oscillations of constant amplitude. The phenomenon is not present for the more idealized linear predation model, suggesting that it can be the source of real ecosystems oscillations.

Keywords: hierarchical competition, predation, bifurcation analysis, ecological cycles

1. Introduction

The use of mathematical models in biology in general and in ecology in particular has grown significantly in the last decade. This is due in part to their predictive capacity, but also due to their power to order and systematize assumptions and thus contribute to elucidate the behavior of complex biological systems. In fact, the interrelation of factors as diverse as climate, access to resources, predators and human activity, makes it necessary to develop mathematical models that allow predicting the effect of each of them on the species involved, showing possible scenarios of coexistence or extinction. A large number of publications on topics such as predator-prey models \[1,2,3\], intra- and...
inter-specific competition \[4, 5, 6\], or habitat fragmentation \[7, 8, 9\] can be found, but more research is still needed on how to integrate all these mechanisms together.

In previous works we developed a mathematical model of extinction and coexistence in a generic predator (or hunter)-prey ecosystem. In order to characterize the general behaviors we focused on a trophic network of three species: two herbivores in asymmetric competition and one predator \[10, 11\]. This problem was studied by means of ordinary differential equations and stochastic simulations. Both approaches provided similar and interesting results. The model predicts the existence of different regimes depending on the parameters considered: survival of one species, coexistence of two and extinction of the third (in the three possible combinations), and coexistence of the three species involved \[10\]. Moreover, the results presented in \[11\] indicate that the superior competitor of the hierarchy is driven to extinction after the introduction of hunters in the model. This happens even in pristine habitats (with no environmental degradation) and, more relevantly, even if the predatory pressure is higher on the inferior herbivore.

In the original model we proposed that predation grew proportionally to the density of herbivores. While this approach is valid for ecosystems with low density of preys, it introduces an unrealistic behavior of the predator population when the density of available prey is high. The model implicitly assumes that the predator or hunter never quench, even when there is an overabundance of prey. In the present work, and in search of a better representation of predation, we analyze a variation of this model. Satiety of the predator or hunter is incorporated in the mathematical description as an asymptotic saturation in the term of predation.

The analysis of this model shows new results. The most interesting aspect of the solutions is the temporal oscillation of the populations. Under certain conditions these oscillations are transient and decay to a stable equilibrium. But in other situations oscillations are maintained indefinitely. In fact, we found regions of coexistence of the three species with persistent oscillations of constant amplitude. These dynamic regimes enrich the predictive properties of the model, so we expect our results to drive the search for evidence of oscillations in populations of current and extinct species.

In the Section 2 we introduce the mathematical model. Section 3 is devoted results, whereas in Section 4 we discuss the main implications of the results and possible future directions.

2. Model with saturation in predation

Our dynamical model requires a set of rules determining the temporal evolution of the system. These rules are inspired by the life history and the ecological interactions of the species involved, corresponding to biotic, environmental and anthropic factors \[10\]. In order to gain insight into the possible outcomes of different scenarios of interest, we have intentionally kept our system relatively simple: two herbivores in a hierarchical competition and a hunter exerting a predatory pressure on both. Some details of the ecological implications are discussed below.

The original model, proposed in \[10\], can be described by the following set of equa-
Each species is described by a dynamical variable: $x_1$ and $x_2$ are the herbivores, and $y$ is the predator. Eqs. (1) describe the time evolution of these variables. We imagine that both herbivores feed on the same resource and therefore compete with each other. This is represented by the first terms of Eqs. (1a) and (1b).

Such competition is asymmetrical, as it happens in most natural situations. This has interesting consequences, since coexistence under these circumstances requires advantages and disadvantages of one over the other. Consider, for example, that the individuals of each species are of different size, or temperament, such that species $x_1$ can colonize any available patch of habitat, and even displace $x_2$, while species $x_2$ can only occupy sites that are not already occupied by $x_1$. In this regard, we call $x_1$ the superior or dominant species of the hierarchy, and $x_2$ the inferior one. Since body size is often the main factor establishing this hierarchy, we imagine that $x_1$ is larger than $x_2$. This asymmetry is reflected in the logistic terms describing the competition in Eqs. (1a) and (1b), as $x_1$ limits the growth of $x_2$ in Eq. (1b), while the reciprocal is not true. This mechanism can be considered as a weak competitive displacement. A strong version of the competitive interaction between the herbivores was also considered in our previous works, consisting of an additional term $-c_1x_1x_2$ in Eq. (1b).

In other words, we have intra-specific competition in both species, but only $x_2$ suffers from the competition with the other species, $x_1$. In this context, for $x_2$ to survive requires that they have some advantage other than size, typically associated with a higher reproductive rate or a lower need of resources.

Besides, the equations for the herbivores also include a mortality term with coefficient $e_i$ and a predation term with coefficient $\mu_i$. The equation for the predator $y$ is also logistic, with a few differences. The reproduction rate of the predator is limited by intra-specific competition but enhanced by the presence of prey.

Now we analyze a variation of the previous model, seeking a more realistic representation of the predation (or hunting) term. The differential equations in the model with saturation are as follows:

\[
\frac{dx_1}{dt} = c_1x_1(1 - x_1) - c_1x_1 - \mu_1x_1y - \frac{\mu_1x_1y}{x_1 + x_2 + d_1}, \tag{2a}
\]

\[
\frac{dx_2}{dt} = c_2x_2(1 - x_1 - x_2) - c_2x_2 - \mu_2x_2y - \frac{\mu_2x_2y}{x_1 + x_2 + d_2}, \tag{2b}
\]

\[
\frac{dy}{dt} = c_yy(x_1 + x_2 - y) - e_yy. \tag{2c}
\]

Observe that, while the predation terms undermine the population of herbivores, predation does not grow proportionally to the presence of prey, but rather saturates if the combined prey population is sufficiently large. This represents a saturation if preys
are overabundant. Note that two new parameters $d_1$ and $d_2$ are included in Eqs. (2), representing the departure from proportionality.

In the next section we present the main results of the model described by Eqs. (2) and compare them with those of Eqs. (1).

3. Results

The study of the system with saturation of the predating pressure shows interesting and much richer results than those of our previous models. While the model described by Eqs. (1) predicts several different regimes, with three and two species coexistence, the steady state solutions are always stable nodes. Here we show that the saturation effect induces oscillatory solutions.

Without losing generality, we have restricted the values of the parameters within a range that shows all the behaviours displayed by the model, especially those scenarios of coexistence between two or all three species. The parameters are chosen in such a way that in the absence of predation pressure ($\mu_1 = \mu_2 = 0$), a coexistence of the three species is achieved. Moreover, the predation pressure over $x_1$ is kept fixed at a value $\mu_1$
Figure 2: Asymptotic solutions for a range of values of $\mu_2$, with A) corresponding to Eqs. (1) (no satiety) and B) corresponding to Eqs. (2) (predation saturation). All the remaining parameters are equal to those of Fig. 1.

< $\mu_2$, corresponding to situations where the inferior species is hunted more frequently than the superior one.

We plot in Fig. 1 the temporal evolution of the population densities for different values of $\mu_2$, the predation pressure over the inferior herbivore, $x_2$. The first panel (Fig. 1a) shows the behavior of the populations when a relatively low predation pressure is exerted on $x_2$, $\mu_2=0.33$. In this case we observe damped oscillations, which converge to the extinction of the superior herbivore $x_1$ and to the coexistence of the other two species, the predator $y$ and the inferior herbivore $x_2$. A higher value of $\mu_2=0.40$ is not enough to allow the survival of $x_1$ but produces sustained oscillations of $y$ and $x_2$ (see Fig. 1b). An even higher pressure on $x_2$ ($\mu_2=0.50$) and the equilibrium between herbivores is achieved, and the three species coexist. This is shown in Fig. 1c, with persistent oscillations of constant amplitude. If we increase further the predation pressure on $x_2$, the oscillations disappear. Still, the coexistence of the three species is possible, as shown in Fig. 1d. As expected, a larger predation pressure on the inferior herbivore will finally produce its extinction, as seen in Fig. 1e. As mentioned before, these non-oscillating behaviors were also observed in our previous model.

In order to provide a visual representation of the steady state behavior of both systems, Eqs. (1) and (2), we show in Fig. 2 the stable equilibria and limit cycles corresponding for the solutions of both models, for a range of $\mu_2$ and the same choice of the values of the rest of the parameters as in Fig. 1. On the one hand the asymptotic solutions corresponding to the model described by Eqs. (1), without saturation in the predation, converge to stable nodes, showing three species coexistence for all the values of $\mu_2$ displayed. These are the set of solutions indicated as A on Fig. 2.

On the other hand, the steady state solutions of Eqs. (2) show both stable nodes and cycles. These are indicated as B on Fig. 2. The dynamics of the cycles is rather
Figure 3: Diagram of coexistence and extinction of the species described by Eqs. (2), as a function of the parameter $\mu_2$. Vertical lines separate the five different regimes observed, corresponding to the named panels of Fig. 1. Upper panel: equilibrium values (dashed lines show unstable equilibria). Lower panel: amplitude of the. Also shown are the two Hopf bifurcations, H1 and H2, and the transcritical bifurcation between two- and three-species cycles. All the remaining parameters are equal to those of Fig. 1.

interesting. For $\mu_2 \lesssim 0.36$ we have non-oscillatory solutions, nodes located on the vertical $(x_2, y)$ plane, that appear as an oblique line of dots in Fig. 2 on the left of the plot. In this regime the dominant herbivore, despite of being less predated on than the inferior one, can not persist. At $\mu_2 \approx 0.36$ there is a Hopf bifurcation and cycles (still on the vertical $(x_2, y)$ plane) appear. Then, at $\mu_2 \approx 0.46$ a new bifurcation occurs. This time it is a transcritical bifurcation of cycles, as will be shown later. The superior herbivore can now coexist with the other two species and the cycle detaches from the $(x_2, y)$ plane. We can observe in Fig. 2 how these twist in the three-dimensional phase space, displaying an oscillatory coexistence of the three species. At $\mu_2 \approx 0.56$ another Hopf bifurcation occurs, this time destroying the cycle, preserving the coexistence between the three species, as shown by the three righmost points of Fig. 2B.

A bifurcation diagram of the phenomenon, using $\mu_2$ as a control parameter, is shown in Fig. 3 where the five regimes of Fig. 1 are indicated by the same letters, in vertical
stripes in both panels. The upper panel displays the equilibria of the solutions. Dashed lines indicate linearly unstable equilibria, and in such circumstances sustained oscillations occur. The amplitude of these oscillations is shown in the bottom panel of Fig. 3.

We can observe more clearly that there is a region where species $x_2$ and the predator coexist (that is, with extinction of the dominant herbivore), corresponding to values of $\mu_2 \lesssim 0.46$. This regime contains the Hopf bifurcation $H_1$, with two-species oscillations for $\mu_2 \gtrsim 0.36$. When the predation pressure on the inferior herbivore is increased above the transcritical bifurcation $TC$ we observe coexistence of the three species, both in an oscillating regime and in a stationary equilibrium, achieved after the Hopf bifurcation $H_2$ is crossed. Finally, if this predation is too high, it is $x_2$ the extinct species, allowing for the survival of the dominant species $x_1$.

![Figure 4: Real part of the eigenvalues corresponding to the linear stability analysis of the equilibria of Eqs. (2) within the range of $\mu_2$ where oscillations are observed. Thick lines correspond to double eigenvalues. All the remaining parameters are equal to those of Fig. 1.](image)

Complementing the bifurcation analysis, we show in Fig. 4 the real part of the eigenvalues of the linearized system at the unstable equilibria in the region of cycles, around the transcritical bifurcation $TC$. Thicker lines (of both colors) correspond to the pair of complex-conjugate eigenvalues of each cycle. Black lines correspond to the two-species oscillation, which is stable for $\mu_2 \lesssim 0.462$. The eigenvalue with negative real part corresponds to the stable manifold of the cycle, which is normal to the plane $(x_2, y)$. At the transcritical bifurcation point $TC$ this eigenvalue exchanges stability with the corresponding one of the other cycle (thin red line), the center manifold abandons the plane $x_1 = 0$ and three-species coexistence ensues.

### 4. Final remarks and conclusions

We have presented here the main results obtained with a simple three-species model, composed of a predator and two herbivores in asymmetric competition, where the predation pressure saturates if the density of preys is high enough. As shown, the model predicts the existence of different regimes as the values of the parameters change. These
regimes consist of the survival of a single species (any of them), the coexistence of two species and the extinction of the third one (the three combinations are possible) and also the coexistence of the three species. But the most interesting aspect of the solutions of this model is that in some cases the populations oscillate in time. Under some conditions these oscillations are transient phenomena that decay to a stable equilibrium. Yet in other situations the oscillations are maintained indefinitely. In fact, we have found regions of coexistence of the three species with persistent oscillations of constant amplitude.

It was shown that, while in the original model without saturation in the predation the asymptotic solutions converge to stable nodes, the steady state solutions of the model with satiation shows both stable nodes and cycles. Our results indicate that, for low predation pressures on the inferior herbivore, the superior one extinguishes and non-oscillatory solutions appear for the remaining species, as indicated by the nodes observed in Fig. 2. At higher predation pressure a Hopf bifurcation and cycles develop, but still the superior herbivore cannot survive. After that, for an even higher value of $\mu_2$, a transcritical bifurcation of cycles occurs to a state of three-species coexistence. In such a context, the superior competitor is the most fragile of both with respect to predation (or to habitat destruction, as shown for example in [11]). For this reason an increase of the predation on $x_2$ releases competitive pressure, allowing $x_1$ to survive. Finally, at an even higher predation pressure, another Hopf bifurcation occurs which destroys the cycle. The coexistence of the three species is preserved until the pressure $\mu_2$ is high enough to extinguish the inferior herbivore $x_2$.

Transcritical bifurcation of cycles in the framework of population models has been found in several systems described by equations that include saturation [12, 13, 14, 15, 16, 17]. Three-species food chain models were extensively studied through bifurcation analysis [12, 13, 14]. A rich set of dynamical behaviors was found, including multiple domains of attraction, quasi-periodicity, and chaos. In Ref. [15] the dynamics of a two-patches predator-prey system is analyzed, showing that synchronous and asynchronous dynamics arises as a function of the migration rates. In a previous work, the same author analyzes the influence of dispersal in a metapopulation model composed of three species [16]. Our contribution, through the model presented here, naturally extends those results in two directions. First, our model has three species in two trophic levels, two of them in asymmetric competition and subject to predation. Second, spatial extension and heterogeneity has been taken into account implicitly as mean field metapopulations in the framework of Levins’ model [5].

Of course, we have not exhausted here all the possibilities of the model defined by Eqs. (2), but it is an example of the most interesting results that we have found. One can also imagine that the cyclic solutions arise from the interplay of activation and repression interactions, as in metabolic systems [18]. The same pattern could be applied to regulations in community ecology if we replace the satiation inhibitor by the addition of a second predator, superior competitor with respect to the other predator, inhibiting its actions. This is a well documented pattern in several ecosystems [19]. We believe that these behaviors are very general and will provide a thorough analysis elsewhere. These dynamical regimes considerably enrich the predictive properties of the model. In particular, we believe that the prediction of cyclic behavior for a range of realistic predator-prey models should motorize the search for their evidence in populations of
current and extinct species.

Acknowledgments

The authors gratefully acknowledge grants from CONICET (PI P 2011-310), ANPCyT (PICT-2014-1558) and UNCUYO (06/506).

References

References

[1] Swihart RK, Feng Z, Slade NA, Mason DM, Gehring TM, Effects of habitat destruction and resource supplementation in a predator–prey metapopulation model, J. Theor. Biol. 210 (2001) 287-303.
[2] Bascompte J, Solé RV, Effects of habitat destruction in a prey–predator metapopulation model, J. Theor. Biol. 195 (1998) 383-393.
[3] Kondoh M, High reproductive rates result in high predation risks: a mechanism promoting the coexistence of competing prey in spatially structured populations, Am. Nat. 161 (2003) 299-309.
[4] Nee S, May RM, Dynamics of metapopulations: habitat destruction and competitive coexistence, J. Anim. Ecol. 61 (1992) 37-40.
[5] Tilman D, May RM, Lehman CL, Nowak MA, Habitat destruction and the extinction debt, Nature 371 (1994) 65-66.
[6] Hanski I, Coexistence of competitors in patchy environment, Ecology 64 (1983) 493-500.
[7] Hanski I, Ovaskainen O, The metapopulation capacity of a fragmented landscape, Nature 404 (2000) 755-758.
[8] Hanski I, Ovaskainen O, Extinction debt at extinction threshold, Conserv. Biol. 16 (2002) 666-673.
[9] Ovaskainen O, Sato K, Bascompte J, Hanski I, Metapopulation models for extinction threshold in spatially correlated landscapes, J. Theor. Biol. 215 (2002) 95-108.
[10] Laguna MF, Abramson G, Kuperman MN, Lanata JL, Monjeau JA, Mathematical model of livestock and wildlife: Predation and competition under environmental disturbances, Ecological Modeling 309-310 (2015) 110-117.
[11] Abramson G, Laguna MF, Kuperman MN, Monjeau JA, Lanata JL, On the roles of hunting and habitat size on the extinction of megafauna, Quaternary International 431B (2017) 205-215.
[12] McCann K, Yodzis P, Bifurcation structure of a three species food chain model, Theor. Pop. Biol. 48 (1995) 93-125.
[13] Klebanoff A, Hastings A, Chaos in three species food chains, J. Math. Biol. 32 (1994) 427-451.
[14] Knettesov YA, Rinaldi S, Remarks on Food Chain Dynamics, Math. Biosciences 134 (1996) 1-33.
[15] Jansen VVA, The dynamics of two diffusively coupled predator-prey populations, Theor. Pop. Biol. 59 (2001) 119-131.
[16] Jansen VVA, Effects of dispersal in a tri-trophic metapopulation model, J. Math. Biol. 34 (1994) 195-224.
[17] Bacelar FS, Dueri S, Hernández-García E, Zaldívar JM, Joint effects of nutrients and contaminants on the dynamics of a food chain in marine ecosystems, Math. Biosciences 218, (2009)24-32
[18] Monod J and Jacob F, General conclusions: Teleonomics mechanisms in cellular metabolism, growth and differentiation, in Cold Spring Harbor Symposia on Quantitative Biology 26 (1961) 389-401.
[19] Terborgh J and Estes JA, Trophic cascades, predators, prey, and the changing dynamics of nature (Island Press, Washington DC, 2010).