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Prey Switching: How to maximize the species's well being

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Abstract: The importance of prey switching in the dynamics of marine ecosystems has been underlined at all levels of the trophic chain: zooplankton species, fish, whales, birds and mammals. Most of the models of foraging behavior emphasize the effects of spatial distribution of populations, much more than the trophic structure of food webs. We propose an economic approach coupling mass balance relationships with the principles of optimal foraging theory and the related ideal free distribution theory. In this model, populations optimize the 'utility' of their diet (the energy gain), being constrained by balance equations between biomasses and trophic flows. This results in a Generalized Nash Equilibrium Problem. More precisely, We are interested in equilibrium of mathematical game given by the situation where all species try to optimize their strategies according to the strategies of all other species.

Keywords: Prey switching, Balance equations, Utility functions, Generalized Nash Equilibrium, Linear Complementarity Problem, Game theory, Networks economics.

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1 Intoduction

The Lotka-Volterra system of equations have been known as a basic model for many types of models that taking into account the interactions of different populations (Alligood et al. 1996; Cosner et al. 1999; Edelstein 1977; Feng et al. 2001; Gold 1977; Gotelli 1988; Gurney et al. 1998; Jansen 1994; Jansen 1995; Jansen et al. 2000a; Jansen et al. 2000b; Jansen 2001; Murray 1977), including the predator-prey interaction of two populations. We add that other concepts such as diffusion and functional response have been taken into account in the Lotka-Volterra equations to gain a better understanding of the dynamics of population interactions (Cosner et al. 1999, Feng et al. 2001, Feng et al. 1997, Gurney et al. 1998; Lu et al. 1997, Murray 1993, Rowell et al. 1996).

The model of Rosenzweig - MacArthur (RM) is a model initially has two equations describing the interactions between a prey and a predator. Historically, this model was used to better understand the dynamics induced by the predations of relationships in the ecosystem. It was then further amended to describe the trophic chain has three levels observed in the middle; this model is given by the system of equations

$$\begin{cases} dV/dt = rV - aV^2 - \frac{kVP}{\chi+V} \\ dP/dt = \frac{\beta kVP}{\chi+V} - mV \end{cases}$$

The new parameter χ is the density of prey at which the predators' kill rate reaches half its maximum. Now we can look at phase portraits for these equations to understand their dynamics. In these pictures, we plot not just a single orbit, but a large number of them.

These are the phase portraits for the models we have considered so far. The density, V, of the prey species is plotted on the horizontal axis, that of its predator, P, on the vertical. The direction of motion is in all cases counterclockwise. (a) The Lotka-Volterra dynamics possess a continuum of periodic orbits. (b) With intraspecific competition, the dynamics have only a single, attracting equilibrium, with damped oscillations relaxing to it. The Rosenzweig-MacArthur model can have a steady state attractor (c) or a limit cycle attractor (d). As before, the steady state attractor corresponds to damped oscillations and ultimately a stable equilibrium population size. The limit cycle, on the other hand, corresponds to sustained oscillations, something like what we see in fluctuating populations.

The implications for population cycles would seem to be clear: Rosenzweig-MacArthur models can have sustained oscillations. Might the observed cyclic fluctuations of boreal mammal populations be due to this sort of interaction? Several scientists have attempted to fit models of this sort to the data, with little success. The difficulty seems to be that the range of parameters over which cycles of the correct period exist is too narrow to explain such a robust phe-

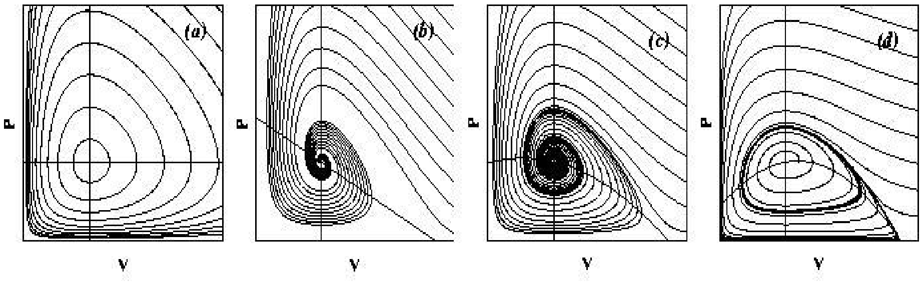

Figure 1: The Lotka-Volterra dynamics.

nomenon. As we will see, this difficulty is related to another oversimplification common to all of the above models.

The first person that used for the first time the term switching is the ecologist W. W. Murdoch in 1969 to describe the situation where a predator eats disproportionately more of the most common type of prey (Murdoch, 1969); but before Murdoch, , exactly eight years earlier in 1962 the geneticist B. C. Clarke described a similar phenomenon and called it "apostatic selection" (Clarke 1962); and since this time, the term prey switching has often been used by ecologists, whereas the apostatic selection has been used by the geneticists, and because of this they have been used to describe different aspects of frequency dependent selection.

One of the ways for described the prey switching is when a predator's preference for a particular type of prey increases as the prey increase in abundance. The result is a strong preference for prey which are common in the environment and a weak preference for prey which are rare.

We can say that the prey switching has been in the scientific literature more than 40 years, but since the first works, the autors have suggested that interest in prey switching has fallen since it is hard to demonstrate whether it has or is occurring (Hassell 2000).

In the present paper, we propose to define a model for 'n' species based on a conventional balance equation $Production = Consumption$. This model is based on many assumptions, including among others: i) middle wealth consistently, ii) no interactions with other species, iii) prey mortality negligible compared to predation rate and iv) no interaction between these predators. The objective of each species is to maximize its income without any consultation of the others, but we have to respect two constraints, the first one is the preservation of the biodiversity and the second one is the posotivity of the trophic flow of each species. With all these considerations, our problem leads to a generalized Nash equilibrium problem, to solve this problem we transform it into a linear complementarity problem and we show that this problem has one and only one solution.

2 A model of prey switching

2.1 Mass balance equations

The prey switching has been used when describing the choice between different species. Our approach is based on a conventional balance equation: *Production* = *Consumption*, more precisely: Assimilated inflow = Mortality due to predation + Somatic maintenance + Other mortality. This model is based on many assumptions, including among others: i) middle wealth consistently, ii) no interactions with other species, iii) prey mortality negligible compared to predation rate and iv) no interaction between these predators.

Production: Let B_i be the biomass of species i; x_{ij} be the trophic flow from species i (prey) to species j (predator); P_i be the assimilated biomass $P_i = g_i \sum_{j=1}^{n} x_{ji}$ where g_i is the trophic assimilation efficiency of species i. For autotroph species, $P_i = g_i E_i$ where E_i is the energy inflow of species i (energy and nutrients, $E_i = 0$ for heterotroph species).

Consumption: A part of the loss of biomass corresponds to the biomass consumed by other species: $Q_i = \sum_{j=1}^{n} x_{ij}$. Other losses R_i, corresponding to somatic maintenance, are assumed to be proportional to biomass: $R_i = \mu_i B_i$ where μ_i is the natural mortality rate of scpecies i. Then, considering that $E_i \neq 0$ and $x_{ji} = 0$ for autotroph species i, that $x_{ij} = 0$ for top predator species and fisheries j.

The mass balance equations of a marine ecosystem is $g_i(E_i + \sum_{j=1}^{n} X_{ji}) = \mu_i B_i + \sum_{j=1}^{n} X_{ij}$. Now we will give the expression of biomass B in function of x_j in matrix form where $x_j = (x_{1j}, ..., x_{nj})^T$.

Expression of B **in function of** x: According to the mass balance equations of a marine ecosystem we have $B_i = \frac{g_i}{\mu_i} E_i + \frac{g_i}{\mu_i} \sum_{j=1}^{n} x_{ji} - \frac{1}{\mu_i} \sum_{j=1}^{n} x_{ij}$.

Otherwise we have i)

$$\sum_{j=1} x_{ji} = x_{1i} + x_{2i} + ... + x_{mi} = \sum_{j=1} e_j^T X_i \tag{1}$$

where e_j is the vector whose all coefficients are zero except that of index j and this coefficient of index j is equal to 1 and ii)

$$\sum_{j=1} x_{ij} = x_{i1} + x_{i2} + ... + x_{in} = e_i^T \sum_{j=1} X_j \tag{2}$$

Using the fact (1) and (2) we have

$$B = diag(\frac{1}{\mu})(GE - \sum_{j=1} A^{(j)} X_j) \tag{3}$$

where G is the $n \times n$ diagonal matrix with $G_{ii} = g_i$ for all i and $G_{ij} = 0$ for all $i \neq j$; $A^{(j)} = I - g.I^{(j)}$ and $I^{(j)}$ is the $n \times n$ matrix with $I_{ik}^{(j)} = 0$ for all $k = 1, ..., n$ and $i \neq j$ and $I_{jk}^{(j)} = 1$ for all $k = 1, ..., n$.

2.2 Utility functions

We define the resulting well being of species j preying species i at level x_{ij} by the following function

$$U_j(X) = \sum_{k=1} x_{kj}(\gamma_{kj} + \alpha_k B_k) + \beta_j B_j. \tag{4}$$

where γ_{ij} is the preference of predator j for prey i; α_i is related to the accessibility of prey i and β_j is related to the togetherness of predator j.

Now we will give the expression of utility functions U_j in function of x in matrix form.

Using the fact that (4) we have $U_j(X) =< X_j; \gamma_j + diag(\alpha)B > +\beta_j B_j$ avec $\gamma_j = (\gamma_{1j}, ..., \gamma_{nj})^T$. According to (3) we have

$$U_j(X) =< X_j; \gamma_j + C(GE - \textstyle\sum_{k=1}^{m} A^{(k)} X_k) > +\beta_j B_j \tag{5}$$

where C is the $n \times n$ diagonal matrix with

$$\begin{cases} C_{ii} = \alpha_i/\mu_i \text{ for all i} \\ C_{ij} = 0 \text{ for all } i \neq j \end{cases}$$

Using the fact $B_j = g_j E_j + g_j \sum_{k=1}^{n} e_k^T X_j - e_j^T \sum_{k=1}^{n} X_k$
we have $U_j(X) =< X_j; \gamma_j + CGE - C\sum_{k=1} A^{(k)} X_k > +\beta_j g_j E_j$
$+\beta_j g_j < \sum_{k=1} e_k, X_j > -\beta_j < e_j, \sum_{k=1} X_k >,$
therefore $U_j(X) =< X_j; \gamma_j + CGE - C\sum_{k=1} A^{(k)} X_k + \beta_j g_j \sum_{k=1} e_k - \beta_j e_j >$
$+\beta_j g_j E_j - \beta_j < e_j, \sum_{k \neq j} X_k >.$

2.3 Constraints

Strategy of species should not result in non-sense situations. There are constraints. Writing that for all species.

For all species j, its predation is enough to get a positive biomass $B(X) \geqslant 0$ that is $A^{(j)} X_j \leqslant GE - \sum_{k \neq j}^{n} A^{(k)} X_k$ and its strategy must be positive $X_j \geq 0$ for all j.

3 Computing the generalized Nash equilibrium

3.1 Generalized Nash equilibrium

Each species trying to maximize its 'Utility function' and achieve a trafic flow that is an optimal response to the trafic flow of the other species. We have a generalized Nash equilibrium where each species's strategy is optimal taking into consideration the strategies of all other species. A Nash Equilibrium exists when there is no unilateral profitable deviation from any of the species involved. In other words, no species would take a different action as long as every other species remains the same. This problem can be translated into the following mathematical problems

For all j we must solve the problem (P_j)

$$(P_j)\begin{cases} Max\ U_j(X) \\ \text{subject to} \\ \qquad\qquad A^{(j)}X_j \leqslant GE - \sum_{k\neq j}^{n} A^{(k)}X_k \\ \qquad\qquad X_j \geq 0 \\ \qquad\qquad (X_k)_{k\neq j} \ \text{ is given} \end{cases}$$

We recall that $(X_1, ..., X_n)$ is called Generalized Nash equilibrium point if and only if for all j, X_j is a solution of problem (P_j) for $(X_k)_{k\neq j}$ is given.

3.2 Linear Complementarity Problem

For all j the essential conditions of Karush-Kuhn-Tucker applied to the problem (P_j) require that if X_j is a solution of the problem (P_j) then there exist constants $u_j \in \mathbb{R}_+^n$, $v_j \in \mathbb{R}_+^n$ and $\lambda_j \in \mathbb{R}_+^n$ such that

$$\begin{cases} CA^{(j)}X_j - \gamma_j - CGE + C\sum_{k=1}^{n} A^{(k)}X_k - \beta_j g_j \sum_{k=1}^{n} e_k \\ \qquad\qquad\qquad\qquad + \beta_j e_j - u_j + A^{(j)T}\lambda_j = 0 \\ A^{(j)}X_j + v_j = GE - \sum_{k\neq j}^{n} A^{(k)}X_k \\ < u_j, X_j > = < v_j, \lambda_j > = 0 \end{cases} \tag{6}$$

It is immediately seen from (6) that

$$\begin{cases} u_j = CA^{(j)}X_j - \gamma_j - CGE + C\sum_{k=1}^{n} A^{(k)}X_k - \beta_j g_j \sum_{k=1}^{n} e_k \\ \qquad + \beta_j e_j + A^{(j)T}\lambda_j \\ v_j = GE - \sum_{k=1}^{n} A^{(k)}X_k \\ < u_j, X_j > = < v_j, \lambda_j > = 0 \end{cases} \tag{7}$$

To maintain the biodiversity of species, it is natural to assume that all biomasses remain positive, that is $B_j > 0$ for all j, therefore $v > 0$. As the scalar product of λ_j and v_j is zero, so $\lambda_j = 0$ for all j. In what follows of this paper, we denote by $v = v_j$. So we have the following expressions

$$\begin{cases} u_j = CA^{(j)}X_j - \gamma_j - CGE + C\sum_{k=1}^{n} A^{(k)}X_k - \beta_j g_j \sum_{k=1}^{n} e_k + \beta_j e_j \\ v = GE - \sum_{k=1}^{n} A^{(k)}X_k \\ < u_j, X_j > = 0 \\ X_j, u_j, v \geqslant 0 \end{cases}$$

Let us denote by $z = (X_1, ..., X_n, 0)^T$, $w = (u_1, ..., u_n, v)^T$

$$M = \begin{bmatrix} 2CA^{(1)} & CA^{(2)} & .. & CA^{(n)} & I \\ CA^{(1)} & 2CA^{(2)} & .. & CA^{(n)} & 0 \\ CA^{(1)} & CA^{(2)} & .. & CA^{(n)} & 0 \\ .. & .. & .. & .. & .. \\ CA^{(1)} & CA^{(2)} & .. & 2CA^{(n)} & 0 \\ -A^{(1)} & -A^{(2)} & .. & -A^{(n)} & 0 \end{bmatrix},$$

$$q = \begin{pmatrix} (\beta_j e_j - \gamma_j - CGE - \beta_j g_j \sum_{k=1}^{n} e_k)_{j=1} \\ (\beta_j e_j - \gamma_j - CGE - \beta_j g_j \sum_{k=1}^{n} e_k)_{j=2} \\ .. \\ (\beta_j e_j - \gamma_j - CGE - \beta_j g_j \sum_{k=1}^{n} e_k)_{j=n} \\ GE \end{pmatrix}$$

then our problem is equivalent to (see Elfoutayeni 2011) the **L**inear **C**omplementarity **P**roblem $LCP(M, q)$:

Find vectors $z, w \in \mathrm{IR}^{n+n^2}$ such that $w = Mz + q \geqslant 0$, $z, w \geqslant 0$ and $z^T w = 0$.

To show that $LCP(M, q)$ has a unique solution it is enough to prove that the matrix M is a $P - matrix$ (Samelson 1958). Recall that a matrix M is called $P - matrix$ if the determinant of every principal submatrix of M is positive (Cottle et al. 1992 and Murty 1972). We can prove by induction that the matrix M is a $P-matrix$; the proof of this result is long and laborious and we chose not to include it in this work; for demonstration we assumed $g_j < 1/n$ for all j. Finally, to calculate this solution. we can use the methods of Y. Elfoutayeni and M. Khaladi (2010, 2012) because of their speed of convergence.

4 A case study

Southern Benguela (Shannon, Jarre-Teichman).

Ecopath model. 10 species.

(Phytoplankton, Meso Zooplankton, Anchovy, Sardine, Squid, Hake, Birds, Seals, Whales, Sharks).

	Phyt	Mizo	Anch	sard	Squid	Hake	Bird	Seal	Whal	Shar
Phyt		4000	14	8						
Mizo		500	20	14	2					0
Anch					1.4	1.5	0.4	0.5	0.2	0.3
Sard					0.5	0.5	0.1	0.1	0.1	0.04
Squid						0.5	0.1	0.1	0.1	0.03
Hake					0.15		0.05	0.1	0.02	0.01
Bird										
Seal							0.01			0.01
Whal										
Shar										

	Biomass	Catch	Outflow	Inflow	g	Mu	Alpha	Beta
Phyt	131.87	-3000	4022	0	2	15	4	0
Mizo	67.83	0	536	450	0.3	12	3	-0.5
Anch	11	2	4.3	34	0.25	0.2	20	0.3
Sard	7.02	1	1.34	22	0.17	0.2	10	0.2
Squi	1.69	0.5	0.83	4.05	0.37	0.1	1	0.4
Hake	1.86	0.25	0.33	2.5	0.27	0.05	1	0.2
Bird	1.28	0	0	0.66	0.1	0.05	1	0.2
Seal	0.7	0	0.01	0.8	0.06	0.05	1	0.05
Whal	0.84	0	0	0.42	0.1	0.05	1	0.1
Shar	0.77	0	0	0.38	0.1	0.05	1	0.2

Discussion

What has been done?

Taking account of the relationships between flows and biomass the whole trophic network, using the principles of optimal foraging theory, we get a simple economical model of the marine ecosystems.

The study of the equilibriums of this model reveals a high sensitivity relative to the definition of utility functions.

A systematic sensitivity analysis reveals that the topological structure of the trophic network is the key point.

It shows the key role of some species (squids or jellyfish in our implementations), which behave at the opposite of keystone species. A very high variability and adaptivity to new situations.

Position of our approach towards OFT

In optimal foraging theory, species switch between preys in a way that maximizes their trophic efficiencies (difference between energy used for predation and energy assimilated after predation). It naturally leads to the ideal free distribution theory: when a predator species consumes simultaneously several species, their trophic advantages are the same. Here we have relaxed the hypothesis that predator choice is determined by trophic efficiency, but by some other quantities. Instead, of saying that nature has selected the most efficient species at all levels, we are considering that it has selected, in a complex network of interactions, some of them that were able to satisfy some constraints.

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