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A GAME THEORY MODEL FOR FOOD WEBS: TIME DEPENDENCE IN A PREDATOR/PREY SYSTEM[1]

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Abstract. A model of an ecological niche is described in which different populations of organisms with trophic interactions involving predator/prey encounters are examined using the notions of food webs and game theory. The reality that species and links are dynamic and change with time is considered. Game theoretical tools are applied to the changing food web structure, where the different "players" are the competing predator populations. Total competition is given by means of payoff functions. The total consumption of the predators, and the biomasses of all prey, are used in the given strategy set. A concept of nucleolar solution is defined which takes into account variation in time. A real predator/prey system is examined and the results of the model are interpreted in ecosystem management terms.

1. Introduction

Models of ecological communities have been considered and developed using the structure of food webs in several publications (e.g. Cohen 1978, Pimm 1982, Post and Pimm 1983, Roberts 1976 and Sugihara 1982, 1983). In this paper I develop a mathematical model that describes the dynamics of food webs using tools of game theory, and find equilibrium values for a community changing through time. In two previous studies (Di Pasquale 1984, 1987) I presented a model for food webs utilizing a static theory, in which the solution was modified for competitive normal games: the nucleolar solution. In this paper, this concept is studied again considering that the web structure changes in time. Thus, trophic interactions involving predator/prey encounters and competition will be studied considering time dependence. The model is also applied to a food web based on real observations of a community to search for equilibrium values for the whole ecosystem and period of study.

2. Model Description

I consider here consumer populations as if they were rational players "choosing" their strategies. That is to say, in terms of game theory the different "players" are the competing predator populations within the ecosystem. The competition here is for food, although the model could easily be modified to consider disputes over territories or other environmental resources. Populations of organisms (which are the "players" in this model) can feed according to any option presented in the strategy set. A strategy is simply one element of a set of possible alternatives, restricted by environmental conditions, that could be chosen by individuals of the populations. These alternatives are related to the biomass of prey species consumed by predators and to the different discrete times.

Biomass values of all prey species are considered to be comparable, so that they can be added. In the following, this assumption is used in introducing the temporal weighted food web matrix. Mathematically a strategy is given by a temporal weighted food web matrix. This is a matrix whose columns correspond to the set of resources or prey in the system, and whose rows correspond to the set of consumers populations. The elements are given by the biomass of the resources used by the consumers for a given time interval. For the first period of time the temporal weighted food web matrix is

$$x^1 = \begin{bmatrix} x^1_{11} & \cdots & x^1_{1k} \\ \cdot & & \cdot \\ \cdot & & \cdot \\ \cdot & & \cdot \\ x^1_{n1} & \cdots & x^1_{nk} \end{bmatrix}$$

where $x^1_{ij} \geq 0$, $\sum_{j=1}^{k} x^1_{ij} \leq x^1_i$, $\sum_{i=1}^{n} x^1_{ij} \leq y^1_j$, $i=1, \ldots, n$, $j=1, \ldots, k$, x^1_{ij} is what population i consumes of j at time 1, thus $x^1_{ij}>0$ if and only if i feeds upon j in the food web R_1. $I=\{1,\ldots,n\}$ is the set of predators or, in terms of game theory, the set of "players". $J=\{1, \ldots, k\}$ is the set of prey populations. x^1_i is the maximum consumption of a population i, given in grams of flesh (carnivores) or dry material of biomass (herbivores).

Since the number of organisms belonging to each prey population is bounded, I consider another restriction: that predator can not consume more organisms in

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the field than are available (no more than y_j^1, which represents the weight of all organisms belonging to population j). Thus, we use the same measure for both x_i^1 and y_j^1.

The strategy set, called X_{R_1} for the first time interval, is the set of all temporal weighted food web matrices. Since some species and links of webs may change through time, while others remain invariant, there will be a sort of dependence among the different periods of time. It is therefore natural to consider that the strategy set for a food web in a determined period depends on the strategies given at the precedent periods. This idea will be now incorporated by our model.

The time we consider here is discrete, represented by $t = 1, \ldots, \ell + 1$. Analogously, we can define as before the strategy set at time w+1 as follows, with $w = 1, \ldots, \ell$. If at time w the option x^w was "chosen" the set $X_{R_{w+1}}(x^w)$ of options or strategies for players (predators) at time w+1 is given as the set of all matrices x^{w+1} of the form

$$x^{w+1} = \begin{bmatrix} x_{11}^{w+1} & \ldots\ldots & x_{1k}^{w+1} \\ \cdot & & \cdot \\ \cdot & & \cdot \\ \cdot & & \cdot \\ \cdot & & \cdot \\ x_{n1}^{w+1} & \ldots\ldots & x_{nk}^{w+1} \end{bmatrix}$$

with $x_{ij}^{w+1} \geq 0$, $x_{ij}^{w+1} > 0$ if and only if i feeds upon j in food web R_{w+1}, $i = 1, \ldots, n$, $j = 1, \ldots, k$. These are further specified by

$$\sum_{i=1}^{k} x_{ij}^{w+1} \leq x_i^{w+1}(x^w) = x_i^w + n_i^w - m_i^w - M_i(x^w) - B_i^w + D_i^w$$

$$\sum_{i=1}^{n} x_{ij}^{w+1} \leq y_j^{w+1}(x^w) = y_j^w + n'^w_j - m'^w_j - M'_j(x^w) - B'^w_j + D'^w_j$$

where:

n_i^w : grams of food consumed by the organisms of population i born in the period w.

m_i^w : grams of food that would be consumed by the organisms of population i which died in the period w.

$M_i(x^w)$: grams of food that would be consumed by the organisms of population i which have fallen prey to predators at time w if the strategy x^w was chosen.

B_i^w : grams that the individuals of population i would eat, which have fallen into a dormant stage.

D_i^w : grams of food that the organisms of population i consume which have returned from a lethargy or dormancy stage.

n'^w_j : weight of individuals of population j born in the period w, given in grams.

m'^w_j : weight of individuals of population j which died in the period w, given in grams.

$M'_j(x^w)$: weight of organisms of population j consumed by predators when strategy x^w was chosen.

B'^w_j : weight of individuals which have fallen into a dormant stage.

D'^w_j : weight of organisms which have returned from a dormant stage.

A niche overlap graph is formed for each time interval with predators $i \epsilon I$. Here whenever i', i'' ϵI (the vertices) overlap with respect to at least one resource, an edge is drawn between them. A connected component of the graph will be a subgraph formed with all vertices linked through edges. Benefit or utility for each consumer is represented by means of its payoff function, which depends both on its own strategy and on the strategies of the other players. The payoff function of a population i is called A_i.

3. Concept of Solution

The main goal will now be to define a concept of solution for the whole period of study. Intuitively this concept gives the best options among the worst possibilities presented, as related to the biomass of all prey populations. These "best trophic positions" will be found by comparing payoff functions for each time in the ecological system. I use a type of nucleolus introduced by Schmeidler (1969), for cooperative games, but modified in my case for the competitive normal games in every period of time. Without considering variations through time, this concept has been used in Di Pasquale and Marchi (1982, 1989) and Di Pasquale (1984, 1987).

Given an element $x^w \epsilon X_{R_w}$, we order the payoff values $A_i(x^w)$ with $i \epsilon I$, so that they are nondecreasing. That is to say, with $i_1, \ldots, i_n$ all the elements of I, we order:

$$A_{i_1}(x^w) \leq \ldots\ldots \leq A_{i_n}(x^w)$$

With these ordered numbers we obtain a vector $\theta(x^w)$. Similarly, given an element $x'^w \epsilon X_{R_w}$ a vector $\theta(x'^w)$ is formed by ordering the values $A_i(x'^w)$ with $i \epsilon I$ as before. At this point payoff functions are arbitrary; specific functions will be defined later.

Compare the first component of $\theta(x^w)$ with the first component of $\theta(x'^w)$, the second component of $\theta(x^w)$ with the second component of $\theta(x'^w)$, and so on. Then say that x^w dominates x'^w and write $x^w > x'^w$, if the first component of $\theta(x^w)$ different from the corresponding component of $\theta(x'^w)$ is strictly greater. The notation $x^w \sim x'^w$ means that all the corresponding components of the two vectors are equal. Similarly define $x^w \gtrsim x'^w$.

We say that $x^w \epsilon X_{R_w}$ is a nucleolar solution if $x^w \gtrsim x'^w$ for each $x'^w \epsilon X_{R_w}$. The set of nucleolar solutions is called N (X_{R_w}).

The solution we have just defined is a static solution, since it does not consider variations with time. To obtain a nucleolar solution which is dependent on time, the solutions obtained in preceding periods should be described. Such a solution will be the temporal nucleolar solution, defined as follows:

We say that

$$x_{1.....\ell+1} = (x^1, x^2, \ldots, x^{\ell+1}) \epsilon X_{R_1} x \ldots x X_{R_{\ell+1}}$$

is temporal nucleolar solution if and only if $x_{1...\ell+1} \gtrsim x'_{1...\ell+1}$ for each $x'_{1...\ell+1} \epsilon X_{R_1} x...x X_{R_{\ell+1}}$. This means

$$x^1 \epsilon X_{R_1},\ x^1 \gtrsim x'^1 \text{ for each } x'^1 \epsilon X_{R_1}$$

$$x^2 \epsilon X_{R_2}(x^1),\ x^2 \gtrsim x'^2 \text{ for each } x'^2 \epsilon X_{R_2}(x^1)$$

$$\vdots$$

$$x^{\ell+1} \epsilon X_{R_{\ell+1}}(x^l),\ x^{\ell+1} \gtrsim x'^{\ell+1} \text{ for each}$$

$$x'^{\ell+1} \epsilon X_{R_{\ell+1}}(x^\ell)$$

That is, every component of the vector that represents the temporal nucleolar solution is solution in the corresponding period. They are linked such that the solution in a determined period follows from solutions in the preceding periods.

4. Construction of Payoff Functions

As we have seen in Section 2 the matrices x^w are formed from elements x_{ij}^w which are zero in the case where i does not consume j in the food web R_w. If i feeds upon j, x_{ij}^w is strictly greater than zero. That is, we assume that the predator i captures at least one prey organism j in the period w. This idea is used in defining the payoffs and finding the corresponding solutions. Thus, the next step is to give a characterization of the payoff functions that represent the "benefit" for each species after choosing their strategies. We will write them for $X_{R_{w+1}}(x^w)$ w = 1, ..., ℓ; X_{R_1} can be given in a similar way by replacing the mentioned sets by X_{R_1}. Let A_i: $X_{R_{w+1}}(x^w) \rightarrow \boldsymbol{R}$ be a continuous function, where $\boldsymbol{R}$ is the set of real numbers. This function is defined such that:

(4.1) For each cluster point $\bar{x}^{w+1}$ of $X_{R_{w+1}}(x^w)$ such that $\bar{x}^{w+1} \epsilon X_{R_{w+1}}(x^w)$, there exist points $x^{w+1} \epsilon X_{R_{w+1}}(x^w)$ such that $A_i(\bar{x}^{w+1}) = A_i(x^{w+1})$. A_i has also the following property

(4.2). We say that A_i has Property B) if for each x^{w+1}, $x'^{w+1} \epsilon X_{R_{w+1}}(x^w)$ such that $A_i(x^{w+1}) < A_i(x'^{w+1})$, it is $A_i(x^{w+1}) \leq A_i(\lambda x^{w+1} + (1-\lambda)x'^{w+1}) \leq A_i(x'^{w+1})$ for all $0 < \lambda < 1$.

Notice that this property generates functions that are more general than the linear functions commonly used.

Intuitively the cluster points are those for which, i being a predator of j, $x_{ij}^{w+1} = 0$. Since $X_{R_{w+1}}(x^w)$ is not compact I propose these payoffs in order to avoid the problem of finding solutions in cluster points that do not belong to this set . Indeed, with the condition (4.1) I will be able to show the existence of nucleolar solutions, given that functions have Property B), formally stated and proved in Theorem 4.1 of the Appendix.

5. Characterizing Nucleolar Solutions

In the previous section we found conditions that secure the existence of nucleolar solutions at each time interval. Since we also need to know how to find these elements exactly, our first aim here will be to give a characterization for such solutions. Our second aim will be to determine when the solutions obtained at each time interval form the temporal nucleolar solution for the entire period of the study. First, let us examine them from an intuitive point of view. In Theorem 5.1 in the Appendix, I present a simple way of finding nucleolar solutions at each time interval, under certain assumptions. The computations are reduced to determining the points that are the maximum of all payoff functions. Corollary 5.2 (also in the Appendix) demonstrates when they are temporal nucleolar solutions. The Theorems I have mentioned, as well as the corollary, will be necessary in order to develop the example in the next section.

6. An Example

The ecosystem studied is situated in Potrero de los Funes, San Luis province, Argentina. The analysis was undertaken in a 500 ha area and only the most important predator/prey species populations in the region were considered. The study is particularly interesting since this area will soon be used for cattle. Thus, my aim here is to study the species interacting in the area with the structure of food webs changing through time. With these groups of organisms an actual food web was constructed, where the arrows point from the populations eaten to the populations that eat them. In this work the period of the study was eight months. This period was subdivided into two time intervals depending on when the most important changes in the populations occur (births, deaths, biological cycles etc.). The first time in-

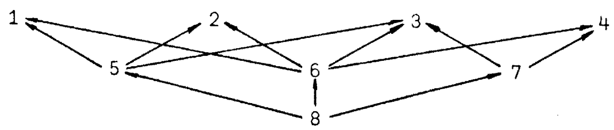

Fig. 1. The food web graph R_1 of a community in San Luis. Numbers 1 to 8 identify populations given in the text.

terval was established from November to February, and the second one from March to June. Most of the data on consumption (values of x_i^w) and weights (values of y_j^w) needed in order to apply the model were obtained in the study area using standard statistical sampling methods. For observations that were impossible to carry out in the study place, data obtained in similar areas judged to be close estimates of the real ones were used.

I begin analysing the community at the first time interval considered. Let the set of predators be

$$I = \{1, 2, 3, 4, 5, 6, 7\}$$

and the set of resources or prey,

$$J = \{5, 6, 7, 8\}$$

where the numbers correspond to the following populations:

1. chimangos *(Milavo chimango)*
2. pirinchos *(Guira guira)*
3. aguiluchos comunes *(Buteo polyosoma)*
4. foxe *(Dusicyon griseus)*
5. grasshoppers *(Dichroplus sp.)*
6. mice *(Acodon sp.)*
7. vizcacha *(Lagostomus maximus maximus)*
8. pasture

The food web R_1 observed is shown in Fig. 1.

The set X_{R_1} of options or strategies for players (predators) corresponding to this food web comprises all temporal weighted food web matrices x^1 of the form

$$x^1 = \begin{bmatrix} x^1_{15} & x^1_{16} & 0 & 0 \\ x^1_{25} & x^1_{26} & 0 & 0 \\ x^1_{35} & x^1_{36} & x^1_{37} & 0 \\ 0 & x^1_{46} & x^1_{47} & 0 \\ 0 & 0 & 0 & x^1_{58} \\ 0 & 0 & 0 & x^1_{68} \\ 0 & 0 & 0 & x^1_{78} \end{bmatrix}$$

such that $x^1_{15}, x^1_{16}, x^1_{25}, x^1_{26}, x^1_{35}, x^1_{36}, x^1_{37}, x^1_{46}, x^1_{47}, x^1_{58}, x^1_{68}, x^1_{78}$ are strictly greater than zero and

$$x^1_{15}+x^1_{16} \leq 180{,}000$$

$$x^1_{25}+x^1_{26} \leq 60{,}000$$

$$x^1_{35}+x^1_{36}+x^1_{37} \leq 90{,}000$$

$$x^1_{46}+x^1_{47} \leq 360{,}000$$

$$x^1_{58} \leq 48{,}000{,}000;\ x^1_{68} \leq 960{,}000;$$

$$x^1_{78} \leq 6{,}480{,}000$$

$$x^1_{15}+x^1_{25}+x^1_{35} \leq 30{,}000{,}000$$

$$x^1_{16}+x^1_{26}+x^1_{36}+x^1_{46} \leq 80{,}000$$

$$x^1_{37}+x^1_{47} \leq 1{,}350{,}000$$

$$x^1_{58}+x^1_{68}+x^1_{78} \leq 106{,}849{,}315$$

The data are given in grams of dry biomass for herbivores and in grams of flesh for carnivores. Thus, the numbers in the first six lines should be interpreted as the maximum consumption of predators during the first time interval. The last four numbers given represent the resources existing in the area given in grams of food or dry material of biomass.

The benefit or utility for predators derived from "choosing" their strategies can be determined by means of payoff functions. I will construct these functions in a simple way. Nevertheless, they could be given and interpreted in another more complex and perhaps more realistic manner. The payoffs are defined below using the data on the maximum consumption of the consumers and the data of biomass of each prey. The payoff corresponding to population 1 (chimangos) is given by

$$A_1\ (x^1) = g_1\ (x^1_{15}, x^1_{16}) + f_{15}\ (x^1_{15}, x^1_{25}, x^1_{35}) +$$

$$+ f_{16}\ (x^1_{16}, x^1_{26}, x^1_{36}, x^1_{46}) + f_{17}\ (x^1_{37}, x^1_{47}) - L_{15}\ (x^1_{15}) -$$

$$- L_{16}\ (x^1_{16})$$

where the consumption function g_1 is defined as

$$g_1\ (x_{15}, x_{16}) = \begin{cases} 3+80 & \text{if } x^1_{15}+x^1_{16} \leq 3+80 \\ x^1_{15}+x^1_{16} & \text{in other cases} \end{cases}$$

Thus, g_1 is a linear function that takes the maximum value when consumer 1 is completely sated and the minimum value when it captures at least one grasshopper whose weight is 3 grams and one mouse whose weight is 80 grams, according to the arguments given

Fig. 2. The niche overlap graph of the community in San Luis. Numbers identify populations given in the text.

in Section 4. The competition functions are given, taking into account the resources shared by the populations belonging to the first connected component, as represented in Fig. 2. In this case the prey species are 5, 6 and 7. In this example the competition functions will be given with the same coefficients in the terms x_{ij} for various i. The competition function based on population 5 (grasshoppers) is defined as

$$f_{15}(x^1_{15}, x^1_{25}, x^1_{35}) = \begin{cases} 3+3+3 & \text{if } x^1_{15}+x^1_{25}+x^1_{35} \leq 3+3+3 \\ x^1_{15}+x^1_{25}+x^1_{35} & \text{in other cases} \end{cases}$$

Again 3 is one grasshopper's weight. The competition functions f_{16} and f_{17} are similarly defined, considering in these cases the corresponding weights of individuals 6 and 7. L_{15} and L_{16} represent the damage caused to the ecosystem by the resources of population 1.

The first damage function L_{15} is defined as a nonincreasing linear function that in the first interval takes its maximum value given by the biomass of grasshoppers (30,000,000 grams), and decreases to zero. Thus, this continuous function is

$$L_{15}(x^1_{15}) = \begin{cases} 30{,}000{,}000 & 0 < x^1_{15} \leq 3 \\ \dfrac{30{,}000{,}000\,(x^1_{15} - 179{,}400)}{-179{,}397} & 3 < x^1_{15} \leq \\ & \leq 180{,}000 - 600 \\ 0 & 180{,}000 - 600 \leq x^1_{15} < \\ & < \min(x^1_1, y^1_5) = 180{,}000 \end{cases}$$

where 3 and 600 (the weight of 200 grasshoppers) are the values I use to divide the interval and give sections where the function is defined as a constant, or intuitively where the damage caused by a grasshopper plague is assumed to be the same. L_{16} is similarly written, with the biomass of mice. The payoffs of 2, 3 and 4 corresponding to the first connected component can be given in a similar way. Consider now the second connected component. Since 5, 6 and 7 feed upon only one resource (pasture), and there is enough for the three populations to eat, their payoffs are simply defined as nondecreasing linear functions which attain their maximum values when the population is completely sated. Notice that all the payoffs I have just defined are particular cases of those defined in Section 4. Theorem 4.1 demonstrates that nucleolar solutions exist, and by Theorem 5.1 it was found that the nucleolar solution at time 1 is the maximum point $x^1 \epsilon X_{R_1}$ such that

$x^1_{15} = 179{,}400$ $\quad x^1_{16} = 600$

$x^1_{25} = 59{,}400$ $\quad x^1_{26} = 600$

$x^1_{35} = 30{,}000$ $\quad x^1_{36} = 15{,}000$ $\quad x^1_{37} = 45{,}000$

$x^1_{46} = 4{,}500$ $\quad x^1_{47} = 355{,}500$

$x^1_{58} = 48{,}000{,}000$ $\quad x^1_{68} = 960{,}000$ $\quad x^1_{78} = 6{,}480{,}000$

As a result, we can see that if the nucleolar solution is attained for the ecosystem in the first time interval, the population of vizcachas would be reduced by its predators by 29.7%, a percentage obtained from the solution knowing the total biomass of vizcachas and the consumption of its predators. In the case of grasshoppers (which is considered a plague by the locals), the population would be reduced by only about 1% by its predators, using a calculation similar to the vizcachas case. Therefore the results obtained may be used to estimate the percentage of population that should be reduced by human control, or the number of predators which must be added to the area to counteract the plague.

Once the nucleolar solution is obtained for the first time interval, the populations in the area in the second time interval are reported. Here, the food web R_2 obtained at this time is the same web as that constructed for the first time interval (Fig. 1). Hence, the niche overlap graph is the same (Fig. 2). Knowing that the option x^1 given previously was chosen, we may now obtain the set of possibilities at the second time interval $X_{R_2}(x^1)$ that depends on it. For these we need first some calculations. I estimated the differences between births and deaths for each population in the first time interval, and calculated the values $M_i(x^1)$ and $M'_j(x^1)$, according to the definition of $X_{R_2}(x^1)$ given at the end of Section 2. Notice that $M_1(x^1) = M_2(x^1) = M_3(x^1) = M_4(x^1) = 0$ because populations 1, 2, 3 and 4 are predators, not prey. The set $X_{R_2}(x^1)$ corresponding to the second period may now be obtained. It comprises all weighted food web matrices x^2 of the form

$$x^2 = \begin{bmatrix} x^2_{15} & x^2_{16} & 0 & 0 \\ x^2_{25} & x^2_{26} & 0 & 0 \\ x^2_{35} & x^2_{36} & x^2_{37} & 0 \\ 0 & x^2_{46} & x^2_{47} & 0 \\ 0 & 0 & 0 & x^2_{58} \\ 0 & 0 & 0 & x^2_{68} \\ 0 & 0 & 0 & x^2_{78} \end{bmatrix}$$

such that x^2_{15}, x^2_{16}, x^2_{25}, x^2_{26}, x^2_{35}, x^2_{36}, x^2_{37}, x^2_{46}, x^2_{47}, x^2_{58}, x^2_{68}, x^2_{78}, are strictly greater than zero, and further:

$x^2_{15}+x^2_{16} \leq 210{,}000$ $\quad$ $x^2_{15}+x^2_{25}+x^2_{35} \leq 14{,}731{,}200$

$x^2_{25}+x^2_{26} \leq 66{,}000$ $\quad$ $x^2_{16}+x^2_{26}+x^2_{36}+x^2_{46} \leq 59{,}380$

$x^2_{35}+x^2_{36}+x^2_{37} \leq 99{,}000$ $\quad$ $x^2_{37}+x^2_{47} \leq 1{,}179{,}000$

$x^2_{46}+x^2_{47} \leq 360{,}000$ $\quad$ $x^2_{58}+x^2_{68}+x^2_{78} \leq 51{,}409{,}315$

$x^2_{58} \leq 23{,}569{,}920$; $x^2_{68} \leq 712{,}560$; $x^2_{78} \leq 5{,}659{,}200$

The payoff functions for predators can now be determined as before, taking into account that in the second time interval, the data on consumption and weight have changed. The reasoning we followed to construct the payoffs for the first time interval is the same, consquently, the payoff functions we have just considered are particular cases of those defined in Section 4. By Theorem 4.1 the existence of solutions is secured.

Using Theorem 5.1 we may write the set of nucleolar solutions, calculating the maximum points of all payoff functions. From this theorem it follows that $N(X_{R_2}(x^1))$ comprises the unique $x^2 \epsilon X_{R_2}(x^1)$ such that

$x^2_{15}=209{,}400$ $\quad$ $x^2_{16}=600$

$x^2_{25}=65{,}400$ $\quad$ $x^2_{26}=600$

$x^2_{35}=39{,}000$ $\quad$ $x^2_{36}=6{,}000$ $\quad$ $x^2_{37}=54{,}000$

$x^2_{46}=4{,}500$ $\quad$ $x^2_{47}=355{,}500$

$x^2_{58}=23{,}569{,}920$ $\quad$ $x^2_{68}=712{,}560$ $\quad$ $x^2_{78}=5{,}659{,}200$

From an intuitive point of view this solution identifies the best strategy, or possibility, that can occur in the field, related to predator consumption in the second time interval, knowing that x^1 was the best option in the first interval. For the solution x^2, and using calculations similar to those used in the first time interval, the population of vizcachas would be reduced by its predators by 34.7% and the grasshoppers by 2.1%. These results can be useful in making managemental decisions. Finally, by Corollary 5.2, we know that (x^1, x^2) forms a temporal nucleolar solution for the whole period of study.

7. Discussion

A mathematical model is presented to describe the predator/prey dynamics of an ecological niche in western Argentina. The species of the ecosystem we studied in a given time interval, and the set of strategies X_{R_1} were obtained using standard methods. The payoff functions were determined in a way related to the ecosystem in order to render the results maximally relevant.

Nucleolar solutions were obtained which can guide human intervention in permitting the individuals of the populations to attain their "best positions" or the "most adequate distribution of food". For example, one may capture and relocate individuals of some populations, or introduce more individuals of other populations. The model registers such interferences as "deaths" or "births", in the second time interval in the construction of the strategy sets depending on the solutions obtained in the first time interval. The procedure explained above for the first time interval is followed for the second interval, and indeed for all the time intervals one is interested in. With the model being capable of responding to interference, I feel it will be useful in decision making that affect natural relations among populations of an area. Indeed, the model should help solving the ecological and biological problems that consider interactions among species in predator/prey systems.

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Appendix

The mathematical results mentioned in Sections 4, 5, and used in the example, are formally stated and proved in this section. Analogously to the way we will give Theorem 4.1, replacing $X_{R_{w+1}}(x^w)$ by X_{R_1} can be used to obtain the existence of nucleolar solutions at time 1.

Theorem 4.1:

If payoff functions are defined as in (4.1) and have Property B), defined in (4.2) then the set of nucleolar solutions $N(X_{R_{w+1}}(x^w))$ at time $w+1$ is nonempty.

Proof: The condition (4.1) secures that for each A_i there exists $x^{w+1} \epsilon X_{R_{w+1}}(x^w)$ such that $A_i(x^{w+1}) \geq A_i(x'^{w+1})$ for each $x'^{w+1} \epsilon X_{R_{w+1}}(x^w)$, that is x^{w+1} is a maximum point of A_i that belongs to $X_{R_{w+1}}(x^w)$. Let (A.1) $\theta(x^{w+1}) = (A_{i_1}(x^{w+1}), .., A_{i_n}(x^{w+1})) = (\theta_1(x^{w+1}), .., \theta_n(x^{w+1}))$ a vector whose components are the payoff values arranged in nondecreasing order as was explained in Section 3. The functions $\theta_i(x^{w+1})$ $i \epsilon I$ are continuous, since payoff functions are defined continuous. Let $C^O = X_{R_{w+1}}(x^w)$

$C^i = \{x^{w+1} \epsilon C^{i-1}$ such that $\theta_i(x^{w+1}) \geq \theta_i(x'^{w+1})$ for each $x'^{w+1} \epsilon C^{i-1}\}$ for $i = 1,\ldots,n$. These sets are nonempty since by definition of payoff functions, condition (4.1) and (4.2) there exists maximum in every set. Obviously $C^n = N(X_{R_{w+1}}(x^w)) \neq \emptyset$ and the existence of nucleolar solutions at time $w+1$ is shown.

The following Theorem can also be shown replacing $X_{R_{w+1}}(x^w)$ by X_{R_1}.

Theorem 5.1:

If there is an element $x^{w+1} \epsilon X_{R_{w+1}}(x^w)$ such that

$$\text{(A.2)} \quad \begin{array}{l} A_{i_1}(x^{w+1}) \geq A_{i_1}(x'^{w+1}) \text{ for each } x'^{w+1} \epsilon X_{R_{w+1}}(x^w) \\ \qquad \vdots \\ A_{i_n}(x^{w+1}) \geq A_{i_n}(x'^{w+1}) \text{ for each } x'^{w+1} \epsilon X_{R_{w+1}}(x^w) \end{array}$$

where $\theta(x^{w+1}) = (A_{i_1}(x^{w+1}),.., A_{i_n}(x^{w+1}))$ is a vector defined as in (A.1), then $x^{w+1} \epsilon N(X_{R_{w+1}}(x^w))$.

Proof: Let $\theta(x'^{w+1}) = (A_{j_1}(x'^{w+1}),.., A_{j_n}(x'^{w+1}))$ a vector formed similar to the vector $\theta(x^{w+1})$. By hypothesis and the definition fo $\theta(x'^{w+1})$ we obtain

$A_{i_1}(x^{w+1}) \geq A_{i_1}(x'^{w+1}) \geq A_{j_1}(x'^{w+1})$.

If $A_{i_1}(x^{w+1}) > A_{j_1}(x'^{w+1})$ then $x^{w+1} > x'^{w+1}$.

If $A_{i_1}(x^{w+1}) = A_{j_1}(x'^{w+1})$, we study the second components of the two vectors. Similarly to the first components, by hypotesis and the definition of $\theta(x'^{w+1})$ we have

$A_{i_2}(x^{w+1}) \geq A_{i_2}(x'^{w+1}) \geq A_{j_2}(x'^{w+1})$.

If $A_{i_2}(x^{w+1}) > A_{j_2}(x'^{w+1})$ then $x^{w+1} > x'^{w+1}$.

In other cases, and using the same reasoning, we can study the third components and so on. Thus, it can be shown that $x^{w+1} \gtrsim x'^{w+1}$ for each $x'^{w+1} \epsilon X_{R_{w+1}}(x^w)$, then $x^{w+1} \epsilon N(X_{R_{w+1}}(x^w))$.

Corollary 5.2:

Let $x^1 \epsilon X_{R_1}$, $x^{w+1} \epsilon X_{R_{w+1}}(x^w)$ for $w = 1,\ldots,\ell$, be elements for which the condition (A.2) holds, then $(x^1,\ldots,x^{\ell+1})$ is a temporal nucleolar solution.

Proof: Trivial from the hypotheses, Theorem 5.1 and the definition of temporal nucleolar solution given in Section 3.

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