## **CAPYBARA:** A Mathematical Model for Population Dynamics including Harvesting

"Regional economies need to incorporate non traditional productive activities which are compatible with the geographic and ecological situation of each region. This will lead to easing the way towards a sustainable management and the long-term conservation of native species and their natural habitats (Quintana, R. & Parera, A. 1994)".

# Introduction

The capybara (*Hydrochaeris hydrochaeris*) is the largest rodent in the world and it is widely distributed in South America with a high potential as an economic resource (hides, meant and oil). Particularly, there are important populations in the region of Esteros del Ibera that could be exploited in a sustainable manner. This could be an attractive possibility for the development of this region since it can help to the conservation of the natural ecosystem, instead of other activities that will impact it in different ways.

A management plan for the use of natural resources requires informed predictions of the ecological effects of resource development, based on the most up-to-date ecological concepts and tools. Designing a management plan requires understanding how the natural environment will respond to the proposed manipulation. In the particular case of wildlife management, a sustainable exploitation requires knowledge of population dynamics for the species, its density in the area, and its vital rates. It is also important to determine which environmental variables lead the dynamics in each region. A mathematical model is a very convenient tool for analyzing possible strategies. Models in a variety of forms play a critical role in advancing our understanding of natural systems. Models abstract basic principles and derive the implications of such abstractions. This provides a method to analyze alternative hypothesis about natural systems responses and the mechanisms that underlie these responses (Gross, L., 2000).

In order to analyze Capybara's Population Dynamics we have began constructing a very simple mathematical model. In this case we have chosen a **stage structured model**. We developed a matrix population model structured in 5 stages. Given the lack of field data about vital parameters, we use iterative fitting methods to estimate some of the parameters involved. The sensitivity and elasticity analysis provide an understanding of the effects of differentiated class-dependent survival and growth probabilities revealing the strengths and the weaknesses within the life cycle.

Finally we add a harvest term in the model in order to analyze different realistic harvesting strategies and we derive conditions for sustainability. The model allows to vary the size of the animals harvested and the season of the year at what the harvest takes place. The model has been implemented in Fortran, with a friendly interface for the user. "Capybara" means "master of the grasses" in the language of the Guarani Aborigines.

# **Biology**

Capybara belongs to Class Mammalia, Order Rodentia, Family Hydrochoeridae, Genus species *Hydrochaeris hydrochaeris*. The Capybara is the largest rodent species in the world, with a mean weight of 50 Kg. Head and body length is 100 to 130 cm., and shoulder height is up to 50 cm. Females are larger than males. Capybaras have no tail, and their fur is long and coarse. They are reddish brown to grayish and are usually yellowish brown on the under side. The limbs are short, the ears are short and round, and the muzzle is heavy. The digits are webbed and have strong claws. The male has an enlarged scent gland on the top of the snout.

These giant rodents are grazing herbivores. They feed primarily on grasses that grow in or near the water plus water plants. They enhance their nutrient intake from food by increasing the efficiency of their digestion, which involves extensive mastication and hindgut fermentation.

Capybaras can breed throughout the year, but they do most frequently at the onset of the rainy season. Gestation requires round 150 days, and generally a female has only one litter per year. The average litter is four. Females give birth on land and young are weaned in about 16 weeks. All females help care for and nurse the young. Sexual maturity is achieved at 18 months approximately. The maximum life expectancy is about 10 years. Copulation takes place in the water, where they need about 40 cm of depth.

Capybaras are social, living in groups of about 20 animals. These units consist of a dominant male, several adult females, their offspring and subordinate males at the periphery of the group. Males who do not have their own family group may be solitarily. Group size tends to be larger in drier areas, and during the drought several hundred individuals may aggregate around the remaining water holes. This situation does not occur in the Esteros del Iberá region where the seasons do not show any lack of water.

Capybaras are most active in the morning and evening. During the hottest part of the day they wallow in shaded wet areas. If startled or pursued on land a Capybara will run and will seek shelter in water if possible. Semiaquatic, they are excellent swimmers. They can swim either with their eyes, ears and nostrils just above water, or they can swim while totally submerged and change directions to confuse the pursuers.

# **A Mathematical Model for Population Dynamics**

In order to analyze the Population Dynamics of Capybara we began constructing a very simple mathematical model. In this case we have chosen a matrix model that describes a simplified life cycle of Capybaras. In many situations, it is essential to recognize the distinct role played by individuals of different age classes or stages. And matrix population models provide a link between the individual and the population, built around a simple description of the life cycle (*Caswell, 2001*). For Capybaras some differences among stages are:

- Predation is important in newborns.
- Harvest can be more convenient in one particular stage
- The fertility of a female could change with age
- Immunity changes with age

Other facts that have been considered:

• Homogeneity within each class is appropriate because of general abundance of the species

• Social organization does not seem to affect reproductive rates or survival.

- Seasonal variations can be easily introduced in such a model.
- Different harvesting strategies can be introduced in the model.

We have developed a model with these main features:

- Discrete in time.
- Time step: seasonal (four steps per year)
- Structured in five stage classes of different duration
- One sex: females

# Simplified Capybara's life cycle

We divide the continuous age variable in five classes. Each class contributes to the other following this scheme.



- <u>Class I</u>: newborn individuals age 0 to 3 months. This class has a high mortality due to natural predators and diseases. This group is nonreproductive and all the surviving individuals in one projection interval go to the second class. Weight ranges from 2.26 kg. to 7.21 kg from the linear regression between age and weight proposed by Ojasti (1973).
- <u>Class II</u>: individuals from age 3 months to 18 months. These individuals are big enough to avoid being eaten by natural predators, so the mortality is lower than in class I. These individuals have not yet reached their

sexual maturity. One Capybara in this class that survives one projection interval either stays in this class or goes to the next one. Weight ranges from 7.21 kg. to 31.96 kg.

- <u>Class III</u>: individuals from age 18 months to 36 months (3 years). These individuals have reached their sexual maturity so this class contributes to class I. One Capybara in this class that survives one projection interval either stays in this class or goes to the next one.
- <u>Class IV</u>: individuals from age 36 months to 60 months (5 years). The individuals belonging to this group are in their best period of fertility and their contribution to class I is the highest. One Capybara in this class that survives one projection interval either stays in this class or goes to the next one.
- <u>Class V</u>: individuals from age 60 months to 120 months (10 years). These individuals contribute to the first class, but in a lower scale than the individuals in the previous class. One Capybara in this class that survives one projection interval either stays in this class or dies.

#### Model Formulation

We have formulated this stage-structured model as a discrete matrix model where the transition matrix entries represent the contributions between classes that can be seen in the previous life cycle. The projection interval is  $\Delta t$  = 3months.

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_{t+\Delta t} = \begin{bmatrix} 0 & 0 & F_3 & F_4 & F_5 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{bmatrix}_{t+\Delta t}$$

where  $P_i$  are the probabilities of remaining in class *i*,  $G_i$  are the probabilities of growing from class *i* to class *i*+1, and  $F_i$  correspond to size specific fertilities.

#### Parameter estimation

Information about the population dynamics of this species is very scarce. The available field information doesn't allow us to estimate survival and growth parameters and to find a correlation with environmental factors that can be important for the dynamics of the species. In this first approach it was absolutely necessary to make some assumptions and to use a simple method in order to estimate the entries of the transition matrix. We used an iterative method proposed by Caswell (1989) for fixed stage duration. An initial growth rate  $\lambda$  is proposed and the matrix entries computed from it. Then  $\lambda$  for the new matrix is calculated and the process can be iterated until satisfactory values of the matrix coefficients are obtained.

The problem is the estimation of the probabilities  $P_i$  and  $G_i$  from length of the stage and the specific survival rates within it. The problem is simplified by introducing two lower level parameters:

 $\sigma_i$  = Probability of survival of an individual in stage *i*.

 $\gamma_i$  = Probability of growth from *i* to *i*+1 given survival.

Hence, in term of these parameters we obtain:

$$G_i = \sigma_i . \gamma_i$$
$$P_i = \sigma_i . (1 - \gamma_i)$$

For this kind of model, Caswell (1989) derives this formulation:

$$\gamma_{i} = \frac{\left(\frac{\sigma_{i}}{\lambda}\right)^{T_{i}} - \left(\frac{\sigma_{i}}{\lambda}\right)^{T_{i-1}}}{\left(\frac{\sigma_{i}}{\lambda}\right)^{T_{i}} - 1}.$$

This equation depends on  $\lambda$  the dominant eigenvalue of the matrix whose entries are being estimated. Thus the iterative method described above is applied once the fertilities are estimated and  $\sigma_i$ 's are given.

The births take place continuously along the year, although an increase in sexual activity has been observed at the beginning of the rainy season *(Mones & Ojasti, 1986; Herrera & Macdonald, 1989; Alho et.al, 1989).* The time for parturition was assumed homogeneously distributed throughout the year, because there are not significant variations in Ibera regarding water availability, which seems to be the driving factor in areas like Pantanal in Brazil, and the rivers and wetlands of Venezuela. Hence the formulas for the fertilities are derived from the classical ones for birth flow population *(Caswell, 1989).* 

$$F_i = \frac{(1+P_i)m_i + G_i m_{i+1}}{2}, \quad i = 3,4 \text{ and } F_i = \frac{(1+P_i)m_i}{2}, \quad i = 5.$$

where the number of female offspring produced by a female in the stage *i* is  $m_i = c_i p \operatorname{sexr} 0.25$ , being  $c_i$  the mean litter size of a female in class *i*, *p* incidence of the parturition and  $\operatorname{sexr}$  the sex ratio of the liter. We assumed  $\operatorname{sexr} = 0.5$ . The factor 0.25 corresponds to the fact that *p* is annual and there are four time steps in one year. Under this formulation, the entry variables of the model are  $\sigma_i$ ,  $c_i$ , and *p*.

# *Growth Rate, Stable Stage Distribution, and Reproductive Value*

From the transition matrix we obtain not only the population numbers projected throughout time, but also other characteristics of the population such as the growth rate, (which is given by the dominant eigenvalue of the matrix), the stable stage distribution, and the reproductive value of each class. We have run simulations for different sets of parameters within reasonable values and observed that outcomes agree with a general pattern of behavior. We take one example as illustration of this general pattern.

## Example

Given the following set of parameters:

Fertility								Survival				
Parameter	$C_1$	C <sub>2</sub>	$C_3$	$C_4$	$C_5$	sexr	р	$\sigma_{_1}$	$\sigma_{_2}$	$\sigma_{_3}$	$\sigma_{\!_4}$	$\sigma_{_5}$
Value	0	0	4	5	3	0.5	1.2	0.65	0.9	0.9	0.9	0.85

We obtain a dominant eigenvalue:  $\lambda$ =1.05906, which corresponds to an Annual Growth Rate of 25.8%. The right and left eigenvectors associated to this eigenvalue give the Stable Stage Distribution and the Reproductive Value respectively.



The population will grow at a rate given by  $\lambda$  (dominant eigenvalue of the transition matrix) and tend to a structure proportional to the stable stage distribution (right eigenvector). In this particular case, approximately 40% of the total population belongs to Class II.

The Reproductive Value measures the value of an individual as a seed for future population growth *(Caswell, 1989)*. Typical reproductive values are low at birth, increase to a peak near the age of first reproduction, and then decline. In this model, the Class IV has the maximum reproductive value. This is due to a relatively higher fertility given by a greater litter size. Management plans should take into account the importance of this class.

## Sensitivity and Elasticity Analysis

An important part of the analysis of the transition matrix is investigating how the results would vary in response to changes in coefficients of the matrix. Such changes represent changes in the life cycle, and may be of interest in several different contexts:

- Measuring "how important" a given initial rate is to population growth.
- Evaluating the effects of error in estimation. Since  $\lambda$ , growth rate, is a function of the  $a_{ii}$ , errors in estimating the  $a_{ii}$  result in errors in  $\lambda$ .
- Quantifying the effects of environmental perturbations. The responses of the vital rates to environmental factors are diverse.
- Evaluating alternative management strategies.

For the values of the parameters as in the example we obtain the following results:





The elasticity of  $\lambda$  with respect to each coefficient of the transition matrix gives the proportional change in  $\lambda$  resulting from a proportional change in that coefficient. From the perspective of proportional sensitivity, the coefficients  $P_{i}$ , the probability of surviving and remaining in Class *i*, are the most important coefficients. Changes in these coefficients will have a larger effect on the value of  $\lambda$ , particularly in Classes II and III.

# **Introducing Harvesting**

Hunting is the main occupation and source of income for many peasants in remote areas of tropical America. These hunters generally hunt on public lands for meat to be sold for local consumption and for skins to be sold to the tanning industry or exported.

In Argentina, Capybaras are hunted mainly for their hides. Capybara skin is of high quality and suitable for gloves, belts, shoes, handbags, and other leather articles. The skin is well priced in Europe for jackets and coats. Limited quantities of salted meat are frequently sold in villages and towns. The only large-scale exploitation of Capybara meat for city markets occurs in the Venezuelan and Colombian "llanos". (Ojasti, J. 1991). Also, its fatty skin is the source of grease used as ointment in pharmaceutical trade. There exists real commercial interest in Argentina for Capybara's meat and leather. *INTA Delta* is developing studies on farming Capybaras and its commercialization.

Considering that a harvesting scenario would be of great interest for Ibera region, we included harvesting in the population model. Harvesting is included in the basic model by determining the proportion of individuals within each class that are harvested in one time interval. Let H a diagonal matrix where its diagonal elements  $h_i$  represent the proportion of individuals extracted from class *i*. Hence the formulation including harvesting is:

$$N_{t+1} = AN_t - \underbrace{H(AN_t)}_{\text{Harvest Term}}$$

This is equivalent to

$$N_{t+1} = \begin{pmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \end{pmatrix}_{t+1} = (A - HA)N_t = (Id - H)AN_t = \begin{pmatrix} 1 - h_1 & 0 & 0 & 0 & 0 \\ 0 & 1 - h_2 & 0 & 0 & 0 \\ 0 & 0 & 1 - h_3 & 0 & 0 & AN_t \\ 0 & 0 & 0 & 1 - h_4 & 0 \\ 0 & 0 & 0 & 0 & 1 - h_5 \end{pmatrix}$$

or

$$N_{t+1} = \begin{pmatrix} 0 & 0 & (1-h_1)F_3 & (1-h_1)F_4 & (1-h_1)F_5 \\ (1-h_2)G_1 & (1-h_2)P_2 & 0 & 0 & 0 \\ 0 & (1-h_3)G_2 & (1-h_3)P_3 & 0 & 0 & \cdot N_t \\ 0 & 0 & (1-h_4)G_3 & (1-h_4)P_4 & 0 \\ 0 & 0 & 0 & (1-h_5)G_4 & (1-h_1)P_5 \\ \hline \\ C & & & \\ \end{pmatrix}$$

Changing the time step, this formulation allows considering harvesting during different seasons. We can model a scenario of *Permanent Harvest*, where the harvesting of the individuals is done during all trimesters and we can keep the same time step:

$$N_{t+\Delta t} = (Id - H). A. N_t = C. N_t.$$

And also we can consider a scenario of *Harvest Seasons*, where the harvesting of the individuals is not done during all trimesters. The extraction can be performed one, two, or three trimesters per year. The formulations for these situations, changing the time step to  $\Delta t = 12$  months, are:

• One trimester per year

$$N_{t+\Delta t} = A^3 \cdot C \cdot N_t$$

• Two trimesters per year

$$N_{t+\Delta t} = A.C.A.C.N_t$$
 (non-consecutive trimesters)  
 $N_{t+\Delta t} = A^2.C^2.N_t$  (consecutive trimesters)

• Three trimesters per year:

$$N_{t+\Delta t} = C.A.C^2.N_t$$
 (two consecutive trimesters)  
 $N_{t+\Delta t} = A.C^3.N_t$  (three consecutive trimesters)

Once the harvesting season is chosen, the percentage of individuals that will be harvested of each population class is given as an entry variable. Depending the commercial goal of the extraction, it is possible that individuals of all classes are not of interest, or individuals of a particular class are more desirable than others. The percentage of harvested individuals can be entered directly using **"Percentage of Harvesting by Class"** or entering the **"Exploitation Pattern"** and the **"Exploitation Intensity"** keys. By Percentage of Harvesting by Class (PHC) we mean the percentage of the population in each class being removed by harvesting. The sum of these percentages does not need to add up to 1. The Exploitation Pattern (EP) is a unit vector (the sum of the coefficients equals 1) that represents the proportion of harvesting carried on each class. The Exploitation Intensity (EI) is the factor that modulates the magnitude of the exploitation vector once the proportions are fixed.

The relationship is:

$$\begin{pmatrix} h_1 \\ h_2 \\ h_3 \\ h_4 \\ h_5 \\ _{PHC} & _{EI} & \underbrace{ \begin{pmatrix} p_1 \\ p_2 \\ p_3 \\ p_4 \\ p_5 \\ _{EP} \end{pmatrix} }$$

"An <u>ecological survey</u> of Capybara populations is the first step required for the management of Capybara for subsistence hunting." (Ojasti)

## Sustainable Harvest

A harvesting policy will be *sustainable* when the dominant eigenvalue  $\lambda$  of the transition matrix is greater than 1. The population will be at equilibrium if  $\lambda = 1$ , but uncertainty in parameter estimates and stochasticity increases the danger that the policy might unintentionally drive the population to undesirable lower levels *(Caswell, 2001).* It has been proved *(Kokko et al. 1996)* that stochasticity increases the risk of population decline and reduces the safe harvest level. Hence, the model should be applied carefully, and more field studies on capybara populations in Ibera region are needed to obtain a more accurate estimation of the parameters.

In a structured classified population, harvest of different stages has different effects on  $\lambda$  and yields different quantities of whatever is being harvested *(Caswell, 2001).* Hence, would be desirable to choose the harvest strategy that is sustainable and maximizes some measure of yield. In this particular model, there are several possibilities for the choice of a harvest strategy and these involve many variables. So, the general maximization problem cannot be solved analytically. Presently, we are working on some of the possibilities under particular assumptions and restrictions.

Regarding the simulation program that might be used as a management tool, once a harvest policy is chosen, the sustainability of the strategy will be specified in the output. We assume that the Exploitation Pattern (EP) is fixed by the interest of the markets and the user will not want to change it. Then, suggestions about how to modify the Exploitation Intensity (EI) in order to make the harvest sustainable, be will be given.

Exploitation on 1 Class with $\lambda = 1$									
Exploitation Pattern	Permanent Harvest	One Harvest Season							
(1, 0, 0, 0, 0)	EI= 0.505	EI=1 and $\lambda > 1$							
Only Class I	# harvested indiv: 492								
(0, 1, 0, 0, 0)	EI= 0.505	EI= 0.6752							
Only Class II	# harvested indiv: 295	# harvested indiv: 318							
(0, 0, 1, 0, 0)	EI= 0.1497	EI= 0.5046							
Only Class III	# harvested indiv: 103	# harvested indiv: 111							
Exploitation on 2 Classes with $\lambda = 1$									
(0, ½, 0, ½, 0)	EI= 0.197	EI= 0.706							
Only Classes II and IV	# harvested indiv: 207	# harvested indiv: 218							
(0, 0, ½, ½, 0)	EI= 0.159	EI= 0.573							
Only Classes III and IV	# harvested indiv: 105	# harvested indiv: 112							

The table shows the results of some runs for different EP and the EI that makes  $\lambda = 1$  in each case. We considered a hypothetical population, which has a growth rate  $\lambda > 1$  without harvest.

# **Conclusions**

This study provides an understanding of the effects of differentiated class-dependent survival and growth probabilities revealing the strengths and the weaknesses within the life cycle. All results point to Class II, females aged 3 to 18 months, to be the one that should receive the widest attention. Also Class III, females aged 19 to 36 months, is important because of its high reproductive value. This knowledge is useful in designing the strategies for sustainable management of this species.

The different results depending on the harvest strategy chosen suggest the usefulness of this kind of model as a management tool. The designing of a good harvest policy would allow the sustainable use of Capybara as a resource with important benefits for the Ibera region.

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Report on the Environmental Impact of the Yacyreta Dam on the Esteros del Ibera, requested by the Undersecretary of Sustainable Developmen and Environmental Policies, Lic. Rubén Patruoilleau, Ministery of Social Action and Environment. October 2000.

Report on the Environmental Impact of the Yacyreta Dam on the Esteros del Ibera, requeste to the University's Rector by the Nation's Attorney of the People. April 2001

## **CONSULTING ACTIVITIES**

Report on the conclusions obtained from research carried on within the INCO DC Project, before the Panel of Experts designated by Entidad Binacional Yacyretá, requested by the Director of Instituto Correntino del Agua, Lic. Delia Acevedo. August 2000.

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Consultant for Sociedad de Propietarios de la Cuenca de los Esteros del Batel-Batelito, Province of Corrientes. Since May 2001. Consultant for Senator Romero Feris and Representative Guillermo Alchouron on the matter of the transfluence Yacyretá-Iberá. June 2001.

Consultant for the Board of Directors of Fundación Vida Silvestre Argentina, on the matter of environmental impact of the Yacyreta Dan on the Esteros del Iberá. July 2001.