SPATIALLY EXPLICIT POPULATION MODELS

During the last decade, ecologists and particularly mathematical ecologists have focused on different approaches to the problem of spatial distribution of species. When the spatial distribution is not considered explicitly, the mathematical models are called spatially implicit. They consider the proportion of territory occupied by given species, but there is no information on which particular sites this occupation takes place (*Caswell & Cohen, 1991; Barradas & Cohen, 1994; Barradas et al., 1996; Barradas & Canziani, 1997; Hanski, 1999; Federico & Canziani, 2000)*. When the spatial distribution of the species is specified, the models are called spatially explicit (*Turner et all., 1995; Marquet & Velasco-Hernández, 1997; Hanski, 1999; Neubert & Caswell, 2000; Ruiz-Moreno et al., 2001)*.

Here we have developed a methodology that allows us to link the information available through vegetation maps, soil maps, and distributed hydrological models to the definition of Habitat Quality Indices for each species of interest. In this way, the population models are not general, but the dynamics of the species is related to each particular environment at a very local scale.

One way to link habitat information (present in the classified synthetic maps or 10-Classes images) with mathematical ecology models is through Spatially Explicit Models. Hence, we developed Spatially Explicit Models based on a Metapopulation approach and from a Cellular Automata perspective. This type of model can describe the spatial distribution of a species in a landscape. The landscape is divided into cells that can be occupied (by a given species) or void. The dynamics of the model results from processes such as Colonization, Persistence, and Dispersion. Both Colonization and Persistence processes are subject to disturbances that can occur with either constant or density dependent probabilities. Several different functional forms that are ecologically meaningful can be considered. Dispersion processes can have global or local range.

Development of the Model

The Model was developed in four progressive stages.

In a first stage, the model was developed taking into account colonization and persistence processes, both affected by disturbance processes, and considering a **global dispersion** process *(Figure 61)*. This *configuration* makes this model comparable with that developed by Federico (1997). This was done in order to verify the performance of the cellular automata. The results of simulations of the cellular automata model for different cases and functional forms show a behavior that coincides to that of the analytical model.
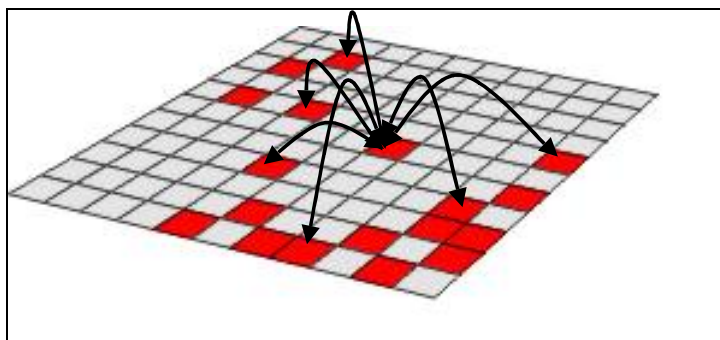
Figure 61. First Stage Cellular Automata Model : Global Rules for
Colonization, Persistence and Disturbances

In a second stage, the model was enhanced with **local dispersion** processes. This restricted range on the dispersion process was necessary because the species can not always spread from one extreme to the other end of the landscape. Clearly, the range allowed for the dispersion depends on the capacity of movement of the species and the time step considered. Under this restriction, all three processes, Colonization, Persistence and Disturbance, in a given cell depend on the state of its neighbors *(Figure 62)*.
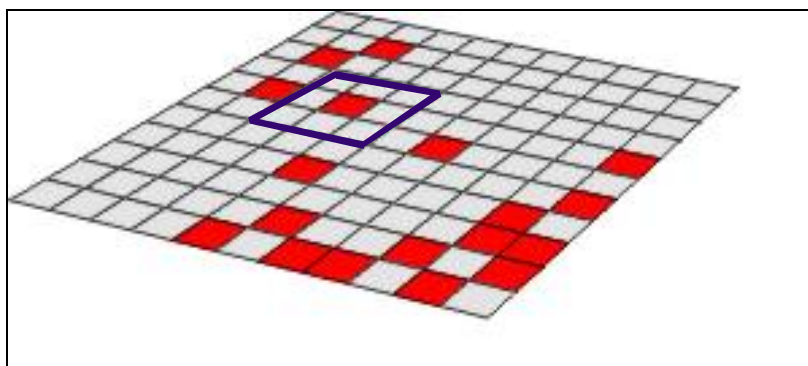

Figure 62. Second Stage Cellular Automata Model: Restricted Neighborhood

Habitat quality affects all the processes (Colonization, Persistence and Disturbance). Hence, the third stage was the incorporation of theoretical habitat qualities, as a first step to the definition of heterogeneity in the landscape. At first, it was necessary to work with a theoretical spatial distribution of habitat quality in order to evaluate the behavior of the model. In Figure 63 a landscape divided into two types of habitat is shown: the red portion has a higher habitat quality than the blue portion. At this point, it is not always possible to use analytical results for a comparative analysis.
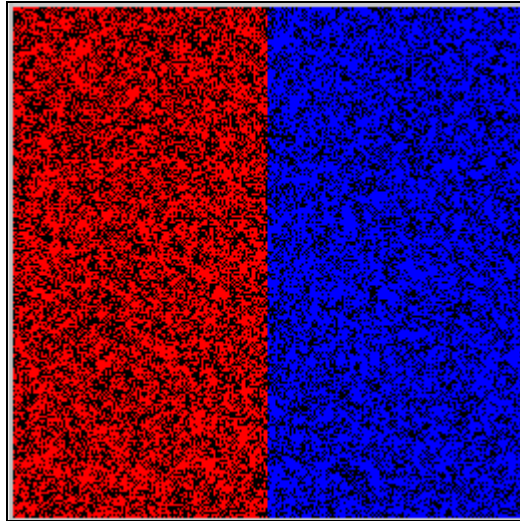
Figure 63. Third Stage Cellular Automata Model: Different Theoretical Habitat Quality in the same Landscape (black points represent species presence)

The fourth stage includes the possibility of running the model on a real landscape. This is done by using a fragment of a 10-Classes image in order to establish the spatial distribution of habitat quality for a given species *(Figure 64)*. This fragment of image is accompanied by a text file were the different habitat quality values are specified. It is appropriate to note that the values of habitat quality should be specified for each species to be modeled. In the case of the species modeled for this project, the capybara and the caiman, it was not possible to establish true habitat quality indices, due to the lack of specific biological and/or ecological information.
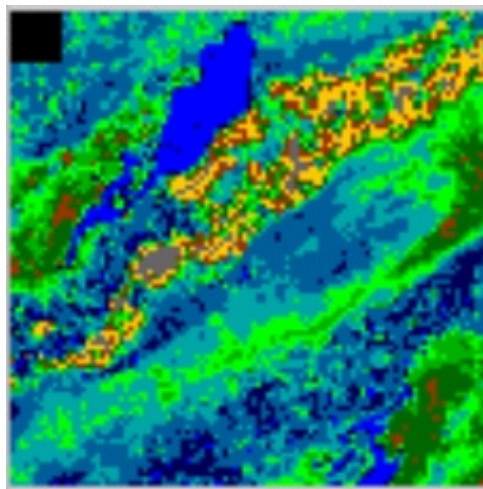

Figure 64. Fourth Stage Cellular Automata Model: Landscape with Habitat Quality from a Synthetic map (black points represent species presence, i.e. here artificial reintroduction)

First Stage Cellular Automata Model

As mentioned earlier, the Analytical Model *(Federico, 1997, Federico & Canziani, 2000)* and the First Stage Cellular Automata Model have very similar behaviors, since from a numerical viewpoint the steady states are almost identical. In fact, the slight differences are due to the introduction of a discretization of the space in the latter relative to the continuous approach in the former model. The most interesting Main result is the possibility of following visually the dynamics of spatial occupation of the landscape.

As an example, consider the following simulation, where the colonization occurs with probability $C(y) = 1 - e^{(-d \cdot y)}$ and where the dispersion coefficient of the Poisson distribution is *d=5.* Disturbances in the colonization process occur with a probability *f(y)* representing a Type III functional response. Disturbances in the persistence of the species in a patch occur with constant probability. The metapopulation model reaches a stable equilibrium when approximately 51% of the patches are occupied.

First Stage Cellular Automata Simulation

Colonization Process $C(y) = 1 - e^{(-d \cdot y)}$ with $d = 5$

Disturbances in Colonization $f(y) = 1 - \dfrac{y^2}{k + y^2}$ with $k = 0.2$

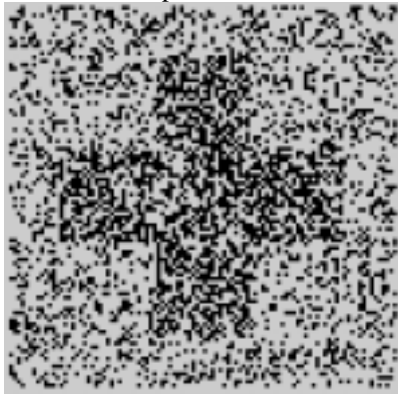Disturbances in Persistence $g(y) = 0.5$

Analytical Steady State $= 0.5107807$

Steady State from Simulation $= 0.51651712$

In the following graphics, it is possible to see how the distribution in space evolves before an equilibrium is reached.
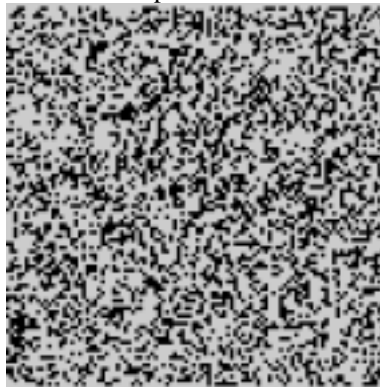
Step Time = 0

Step Time = 1

Step Time = 2

Step Time = 17 (Steady state)
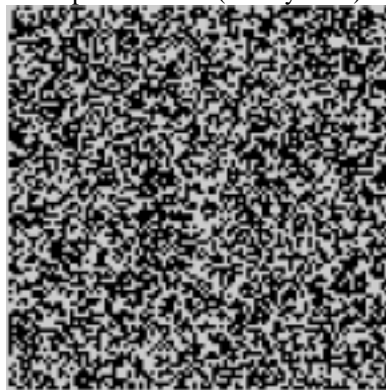
Second Stage Cellular Automata Model

Second Stage Cellular Automata Model have similar behavior to the previous model and the type and value of the steady states are similar to those of the previous one. The main result is that now we have the possibility of evaluating how the initial spatial distribution of the species in the landscape affects the time to reach steady states.

Consider the following second stage cellular automata simulation, where the probability of colonization is no longer Poisson, but constant, all the other functions remaining as in the previous example. We can observe in the figures that it takes a much longer time to occupy the landscape.

First Stage Cellular Automata Simulation

Colonization Process $C(y) = \mu = 0.92$

Disturbances in Colonization $f(y) = 1 - \dfrac{y^2}{k + y^2}$ *with* $k = 0.2$

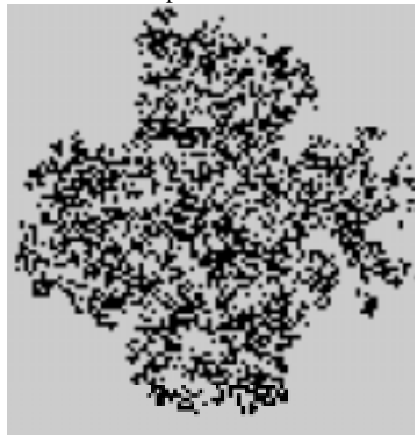*Disturbances in Persistence* $g(y) = 0.5$

Neighborhood Definition : Moore

Analytical Steady State $= 0.5107807$
Steady State from Simulation $= 0.4586507$
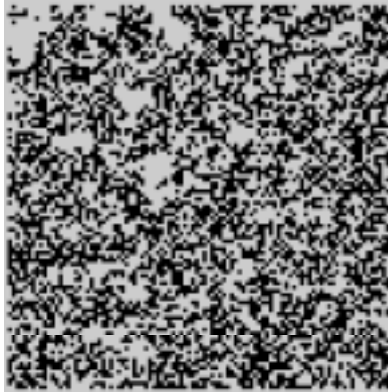

Step Time = 0

Step Time = 37

Step Time = 7

Step Time = 182 (already in a Steady State)

This model is a good approximation to many real life situations, where the processes are local but their consequences are observed at the global scale. At this stage, the model has some significant theoretical applications, because it allows to observe some interesting effects, such as the formation of some areas of higher density, where the species can consolidate its presence and from which it becomes easier, either to colonize or to resist extinction.

As mentioned earlier, the model can be used as a tool to select the location or locations of a re-introduction of a species in a given homogeneous area, in order to insure a better probability of success, as can be observed in *Figure* 65.
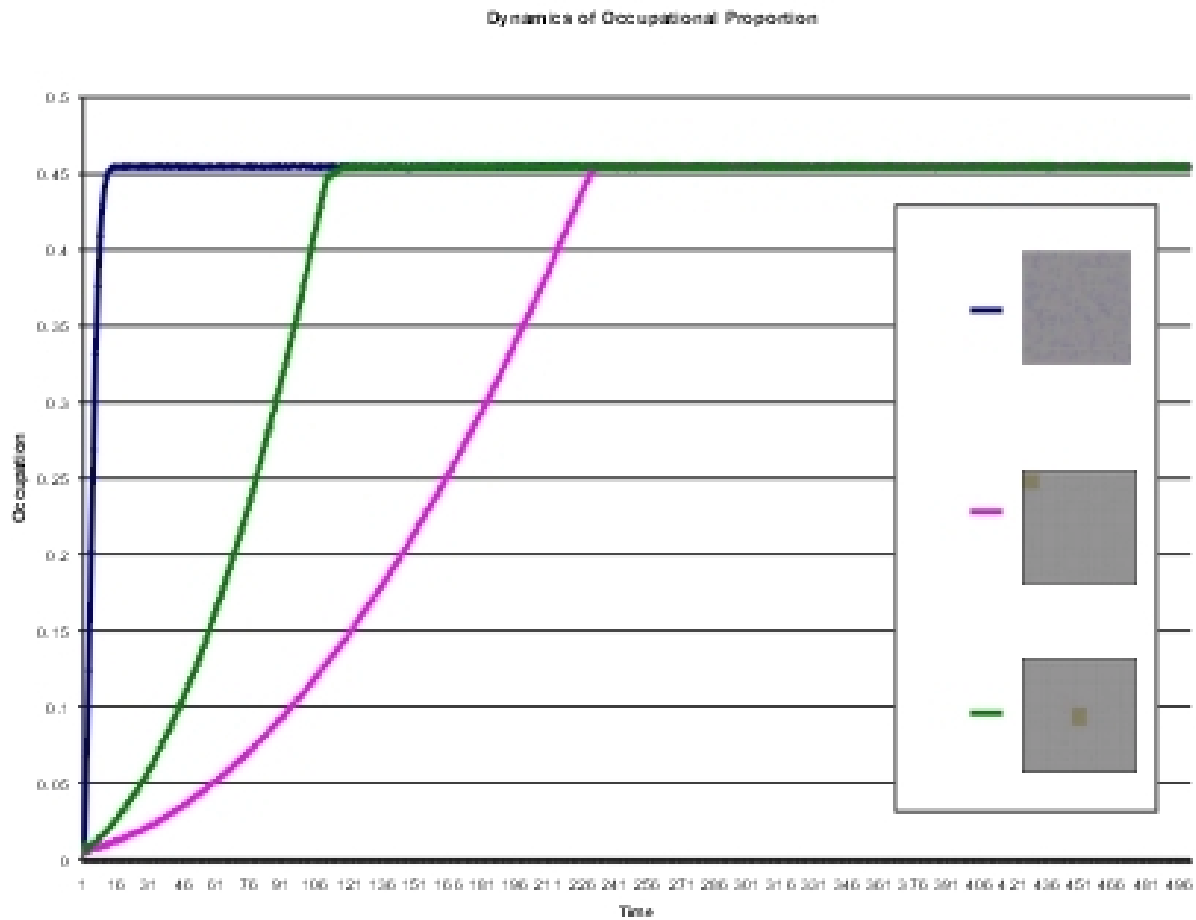
Figure 65. Notable Differences in the time needed to reach a steady state depending on the initial location (random in blue, from a corner in rose, from the center in green)

Cellular Automata with Heterogeneous Habitats

Although the construction of spatially explicit population models is flourishing, very little has been done regarding the inclusion of habitat heterogeneity. We believe that the cellular automata approach is very appropriate for the study of this type of problems because it simplifies the formulation of the interactions between cells *(Wolfram, 1986).* The recent literature shows some intents of formulating models that are continuous in time and discrete in space, as well as others that are discrete in time and continuous in space, but the mathematical treatment becomes cumbersome very rapidly, and can not be applied to real-life situations.

The behavior of the **Third and Fourth Stage** Cellular Automata Models here developed strongly depends on habitat quality indices, distribution, and relative abundance of the species. Using third stage models we can develop

theoretical computational experiments that help understand at a smaller scale the processes involved. These are useful to study afterwards the behavior of the fourth stage models that involve several different habitat qualities from satelital images. Otherwise, the complexity of the interactions occurring at that stage could hinder the interpretation.

Consider now a simulation example for the third stage model. As previously, all the functions remain the same, but the landscape is now defined into two different regions with a higher quality for the red one and a lower quality for the blue one. Now it is possible to observe the differences in movements of the species and the time needed to expand, based not on the species ability but only on habitat factors.

Third Stage Cellular Automata Simulation

Colonization Process $C(y) = \mu = 0.92$

Disturbances in Colonization $f(y) = 1 - \dfrac{y^2}{k + y^2}$ *with* $k = 0.2$

Disturbances in Persistence $g(y) = 0.5$

Neighborhood Definition : Moore

Red Region Habitat Quality $\approx + 50\%$

Blue Region Habitat Quality $\approx - 50\%$

Step Time = 0

Step Time =10
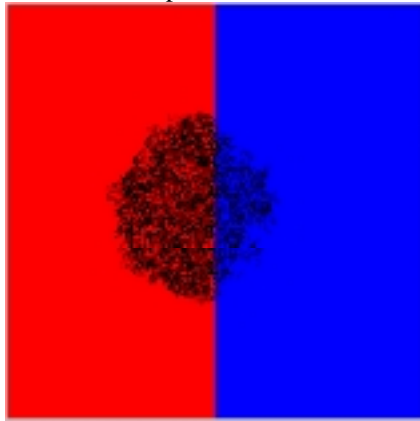
Step Time = 50

Step Time = 188
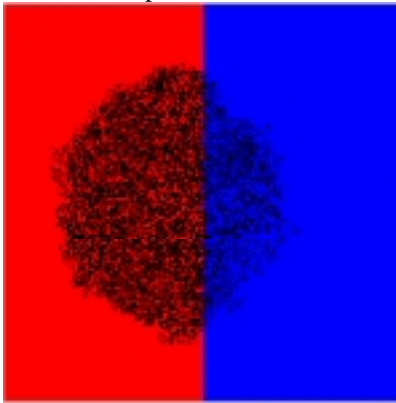
A similar experiment can be carried on now for the fourth stage model, taking as landscape a sector of the classified synthetic map of the Esteros del Ibera, near the Parana Lagoon, on the western region of the system. The habitat classification corresponds tentatively to capybara populations.

Fourth Stage Cellular Automata Simulation

Colonization Process $C(y) = \mu = 0.92$

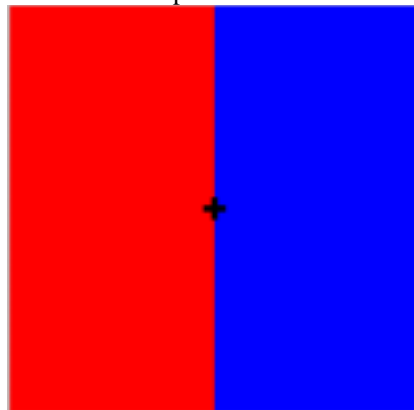*Disturbances in Colonization* $f(y) = 1 - \dfrac{y^2}{k + y^2}$ *with* $k = 0.2$

Disturbances in Persistence $g(y) = 0.5$
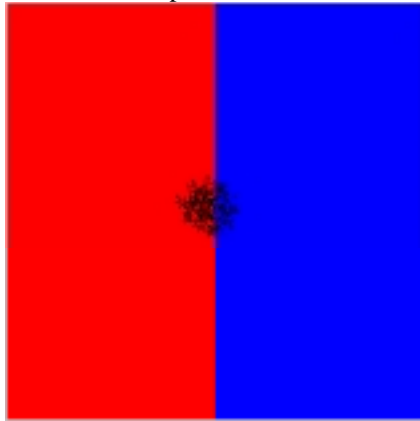
Neighborhood Definition : Moore

Region Habitat Quality from Synthetic Maps

Step Time = 0

Step Time = 10
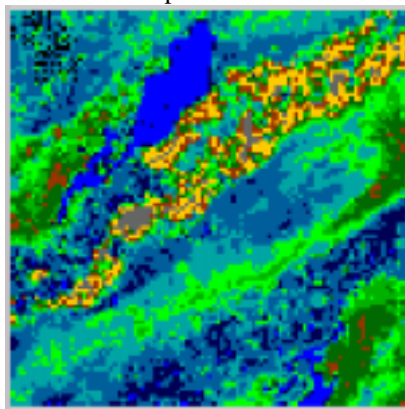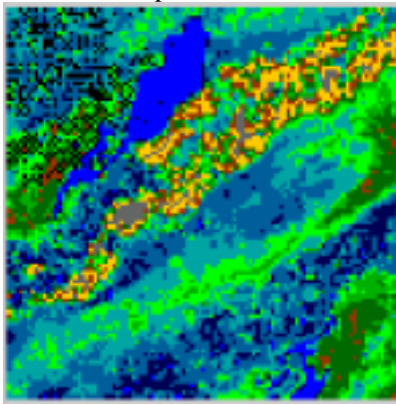
Step Time = 50

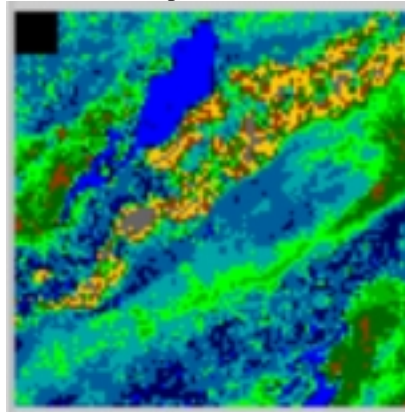Step Time = 185
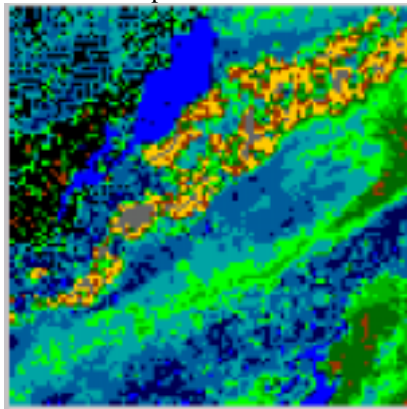
Both types of model allow to analyze the time required to reach steady states and how the initial spatial distribution can have an influence on it. It is also possible to perform experiments regarding the implementation of controls over any given area within the landscape considered.

Any of these Cellular Automata Models can be a decisive tool in situations such as the re-introduction of species. The models we developed are the first link between ecological data and an integrated management tool that provides analysis of spatial distribution, efficiency and efficacy of re-introduction, economic issues, and control of the presence of a species in specific places.

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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.

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.
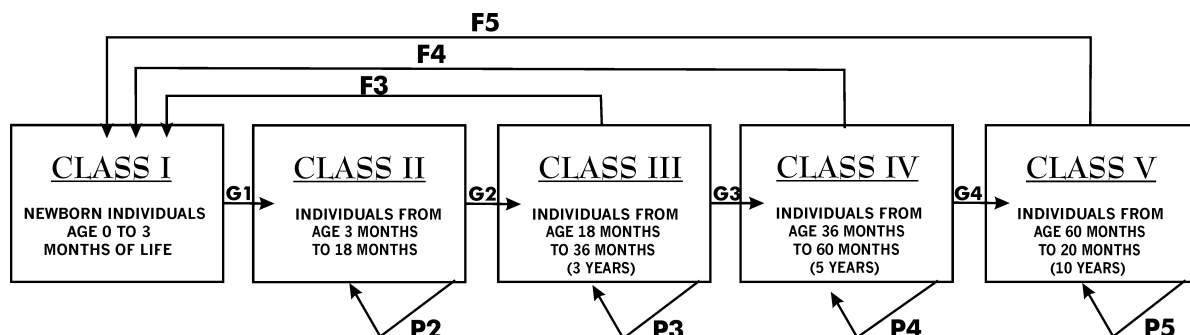
Class I: newborn individuals age 0 to 3 months. This class has a high mortality due to natural predators and diseases. This group is non- reproductive and all the surviving individuals in one projection interval go to the second class. Weight ranges from 2.26 kg. to 7.21 kg from the linear regression between age and weight proposed by Ojasti (1973).

Class II: 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.

Class III: 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.

Class IV: 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.

Class V: 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 $\Delta t = 3$ months.

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

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 λ is proposed and the matrix entries computed from it. Then λ 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:

σ_i = Probability of survival of an individual in stage *i*.

γ_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:

$$\gamma_i = \frac{\left(\sigma_i / \lambda\right)^{T_i} - \left(\sigma_i / \lambda\right)^{T_i - 1}}{\left(\sigma_i / \lambda\right)^{T_i} - 1}.$$

This equation depends on λ 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 σ_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 $m_i = c_i \, p \, sexr \, 0.25$, being c_i the mean litter size of a female in class i, p incidence of the parturition and *sexr* the sex ratio of the liter. We assumed *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 σ_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_2	C_3	C_4	C_5	sexr	p	σ_1	σ_2	σ_3	σ_4	σ_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: λ=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.
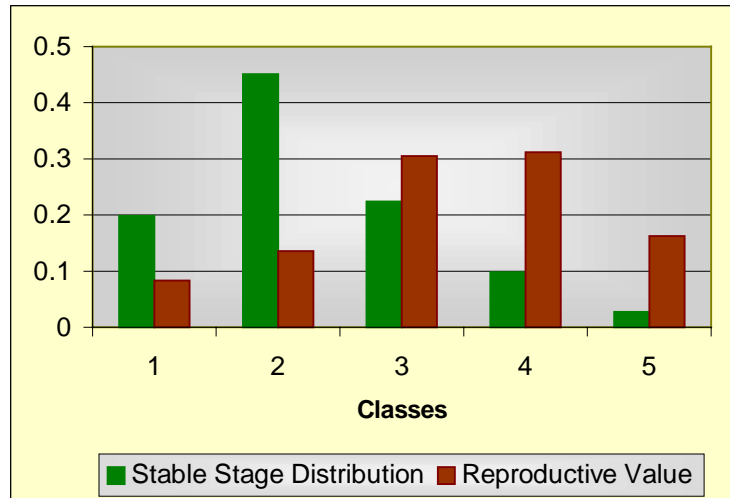
The population will grow at a rate given by λ (dominant eigenvalue of the transition matrix) and tend to a structure proportional to the stable stage distribution (right eigenvector). In this particular case, approximately 40% of the total population belongs to Class II.

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 λ, growth rate, is a function of the a_{ij}, errors in estimating the a_{ij} result in errors in λ.

- 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:

Dominant Eigenvalue Elasticities

Lower Level Elasticities
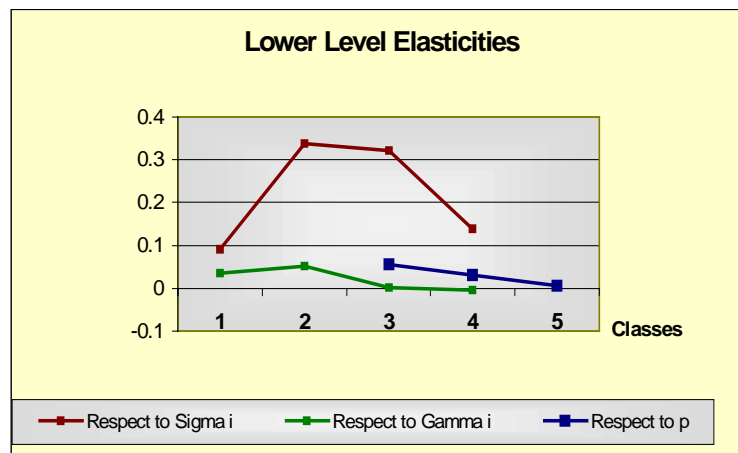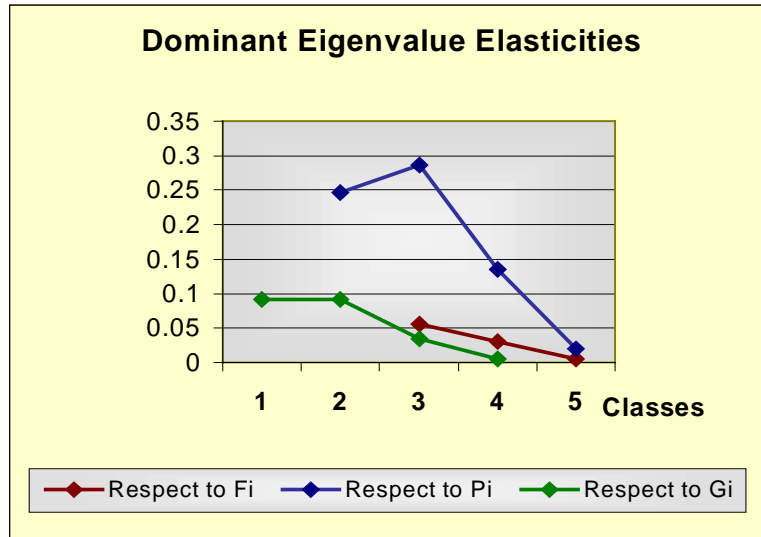
The elasticity of λ with respect to each coefficient of the transition matrix gives the proportional change in λ resulting from a proportional change in that coefficient. From the perspective of proportional sensitivity, the coefficients P_i, the probability of surviving and remaining in Class i, are the most important coefficients. Changes in these coefficients will have a larger effect on the value of λ, 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

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

or

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

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 $\Delta t = 12\,\text{months}$, are:

- One trimester per year

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

- Two trimesters per year

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

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

- Three trimesters per year:

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

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

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:

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

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