

**A STAGE-STRUCTURED MODEL WITH TWO  
TIME-STEPS FOR ANALYZING THE POPULATION  
DYNAMICS OF RHEA AMERICANA UNDER  
VARIABLE ENVIRONMENTAL CONDITIONS**

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**ABSTRACT.** The Ñandú or *Rhea americana* is an autochthonous species perfectly adapted to the pampas environment and only distributed in South America. The species exhibits an unusual breeding system combining polygyny, polyandry, communal nests and exclusive male parental care, which seems to contradict the idea of selfish genes. Our aim has been to construct a mathematical model based on the short term population dynamics of Rhea, living in the wild or in semi-captivity, and taking into account environmental factors that vary from year to year. Due to the characteristics of its life cycle, it was necessary to develop a model that allows us to differentiate between the survival and fertility rates of each age group and the distinct behavior during breeding and non-breeding seasons. Therefore, a quarterly differentiated stage-structured discrete model was needed. Time steps of different lengths are used for modeling chicks or “charos” on the one hand, and juveniles and adults on the other. Environmental variables have been incorporated into the model because they affect the reproductive success of the species. Different scenarios are given as illustrations of the model use. Finally, the possibility of harvesting has been introduced in the model. The model is intended as a first step towards more refined models and systematic data gathering with the purpose of leading the way to a computational tool for risk assessment and decision-making.

**KEY WORDS:** *Rhea americana*, stage-structured matrix models, population dynamics.

**Introduction.** *Rhea americana* is an autochthonous species in South America. The development of agriculture has caused a decrease in the wild population densities owing to farmers forcing the individuals out of the fields, claiming damage to crops and competition with livestock in pastures. There have been some investigations carried out and the results show that such competition is insignificant (Vacarezza et al. [2001], Uhart and Milano, [2002]). This is the reason for attempting to convince farmers that the ñandú can be considered an attractive and sustainable management option that could become a profitable economic resource, while at the same time contributing to its conservation.

Stage-structured matrix models are used when the individuals of a population exhibit different fertility and survival rates at different stages. Hence, it is essential to recognize the distinct roles played by individuals at different stages of development. A matrix population model provides a link between the individual and the population, built around a simple description of the life cycle (Caswell [2001]). In this particular case, such models seem very appropriate for including environmental parameters that affect the reproductive success in a direct and simple manner. Nevertheless, the representation of the reproductive process requires a careful refinement in the time steps in order to adequately reflect parental behavior and offspring survival and, at the same time, take full advantage of the simplicity of a matrix model.

**Rhea americana, its life history.** *Rhea americana* belongs to the Family Rheidea, Order Rheiformes, Superorder Paleognathae. This species is perfectly adapted to the pampas environment. It is one of the oldest and biggest birds of America. The male can measure up to 150 cm in height and weigh up to 35 kg, while the female reaches 130 cm and 25 kg (Cajal et al. [1993], Fernández [1998]). Historical references can be found in Azara [1850], Muñiz [1885] and Meyer de Schaunsee [1966]. In the wild, they can live up to 15 years (Davel [1911], cited in Fernández [1998]) but it is not known whether they are able to reproduce at advanced age. When they are kept as pets they can live up to 40 years (Dani [1993]).

The social structure changes with the time of the year. Rheas are gregarious and form groups of 2 to 3 animals, and even flocks of over

50 during the non-breeding season (May–August). With the first warm days when spring approaches, these groups begin to fragment to form the breeding groups (September–December) (Bruning [1974]).

The mating system of the ñandú combines polygyny and polyandry. The male simultaneously monopolizes various females which mate and lay eggs sequentially in nests of different males. The size of the nest depends on the number of females that form the harem, generally 6 to 8. However, harems with 2 up to 15 females can be seen.

The male is the one which carries out the largest part of the reproductive work as he builds the nest, rolls the eggs into the nest with his bill, incubates them (for a period of about 40 days) and takes care of the chicks (“charos”) until they are two to three months old (Bruning and Dolensek [1986]). The success of the nest, e.g., that some eggs hatch, depends basically on the fitness of the male incubating them. Some males begin the breeding activities at the beginning of the breeding season, while others choose to start them at the end.

The participation of the female is restricted to the setting of eggs (Bruning and Dolensek [1986]). The quantity of eggs produced is limited by the energy capacity of each female. When the setting in one given nest concludes, the females who form that harem join with another male that has followed them during this period. The male guides them to his nest and another cycle begins.

Births begin in early November and continue until late February. During the first months of life mortality is high, particularly during the first days after hatching, and an asymptote is reached in about one month (Fernández [1998]). The mortality of chicks as well as the abandonment of nests are caused by natural predators and by adverse environmental conditions.

During the breeding season, the principal predators are lizards, weasels, foxes and armadillos who prey on the eggs, while the common predator of chicks are wild birds (caranchos, chimangos) as well as dogs that intrude when small birds are far from their fathers (Milano, pers. comm.).

In this species’ population dynamics, the climatic factors have a great importance during the whole year. During the breeding season, intense droughts can dehydrate the eggs and abundant rains can flood the nests, stimulating abandonment in both cases. The rest of the year, the birds

must obtain the necessary energy to carry out all the activities linked to their survival and that of their species.

**The mathematical model for population dynamics.** Due to the fact that reproductive and survival rates are not the same for all individuals, a stage-classified matrix model has been built for studying the population dynamics.

The breeding success depends mostly on the male because he is the one who takes and incubates the eggs, and then cares for the chicks during the first months of their life. For this reason only the male population will be modeled. The relationship female:male has been considered 1:1 in *Rhea americana* populations.

The model is discrete in time. The population has been structured in five stages of different duration, with the purpose of obtaining a better assessment of the population due to factors that take place seasonally (quarterly). The model is in fact composed of six matrices: four transition matrices for juveniles and adults and two for hatching and chicks. These matrices are combined by means of products and sums in order to produce the annual matrix. The adult transition matrices reflect changes in the population every three months, while the other two, devoted to the reproductive process, have a ten-day time step and generate the new individuals that enter the population. The  $n$ th ten-day interval will be referred to as  $n$ th-decade.

All of these matrices are necessary because the reproduction is not continuous during the year but takes place in the warm season. Also, the individuals change stages at different months of the year, depending on when they are born.

Harvest has been introduced in the model by means of a diagonal matrix, making it possible to study different harvest scenarios.

**Simplified life cycle and model formulation.** The population has been divided in five stages as shown in Table 1. In the model, chicks are counted for the first time in the population in April or July, depending on whether they came from eggs that began to be incubated at the beginning of the breeding season or later in the same season. Since the chicks must be at least three months old to be considered

part of the population, all individuals are between 3 to 6 months old when they are counted for the first time, as they enter the *charos* stage.

We have observed that the individuals that enter the adult population model in April grow from one stage to another during the period January–April, while those that enter in July grow from one stage to another during the period April–July. During the other periods, they remain in the same stage.

The quartile projection matrices that reflect this situation take the form:

$$A = \begin{bmatrix} a_{11} & 0 & 0 & 0 & 0 \\ 0 & a_{22} & 0 & 0 & 0 \\ 0 & 0 & a_{33} & 0 & 0 \\ 0 & 0 & 0 & a_{44} & 0 \\ 0 & 0 & 0 & 0 & a_{55} \end{bmatrix}, \quad B = \begin{bmatrix} b_{11} & 0 & 0 & 0 & 0 \\ b_{21} & b_{22} & 0 & 0 & 0 \\ 0 & b_{32} & b_{33} & 0 & 0 \\ 0 & 0 & b_{43} & b_{44} & 0 \\ 0 & 0 & 0 & b_{54} & b_{55} \end{bmatrix}$$

$$C = \begin{bmatrix} c_{11} & 0 & 0 & 0 & 0 \\ c_{21} & b_{22} & 0 & 0 & 0 \\ 0 & c_{32} & c_{33} & 0 & 0 \\ 0 & 0 & c_{43} & c_{44} & 0 \\ 0 & 0 & 0 & c_{54} & c_{55} \end{bmatrix}, \quad D = \begin{bmatrix} d_{11} & 0 & 0 & 0 & 0 \\ 0 & d_{22} & 0 & 0 & 0 \\ 0 & 0 & d_{33} & 0 & 0 \\ 0 & 0 & 0 & d_{44} & 0 \\ 0 & 0 & 0 & 0 & d_{55} \end{bmatrix}$$

where  $A$  is the projection matrix from October to January,  $B$  from January to April,  $C$  from April to July and  $D$  from July to October. The population that has been projected annually is that of October because this is the month for reproduction.

Once the quartile projection matrices have been constructed, the annual matrix is obtained as their product. Hence, the annual projection matrix without breeding is  $D.C.B.A$ .

Since the chicks are generated by the October population only, two matrices need to be built. The matrix  $\mathbf{P}$  permits counting the individuals that are added to the population in April and the matrix  $\Theta$  those added in July. The only non-zero line of these matrices is the first, basically because the matrices correspond to the first line in an ordinary Leslie or stage-structured matrix.

The coefficients of matrices  $\mathbf{P}$  and  $\Theta$  have been obtained by working with the following variables and parameters:

- $\mathbf{R} = (\mathbf{r}_1, \mathbf{r}_2, \mathbf{r}_3, \mathbf{r}_4, \mathbf{r}_5)$ , where the  $j$ th component corresponds to the probability of a male nesting during the  $j$ th stage ( $j = 1, 2, \dots, 5$ ).

- $\mathbf{d}_i$  is the probability of starting incubation during the  $i$ th decade ( $i = 1, 2, \dots, 9$ ).
- $\mathbf{h}_i$  is the probability of carrying out a successful hatching during the  $i$ th decade ( $i = 1, 2, \dots, 9$ ).
- $\mathbf{g}_i$  is the probability of growing from decade  $i$  to decade  $i + 1$ , ( $i = 1, \dots, 8$ ).
- $\mathbf{e}(\mathbf{i})$  is the discrete function that represents the environmental conditions during each of the nine decades that belong to the hatching season. This function can take five possible values depending on whether the decade is very dry, dry, normal, humid or very humid.
- $\mathbf{N}(\mathbf{t}) = (\mathbf{n}_1, \mathbf{n}_2, \mathbf{n}_3, \mathbf{n}_4, \mathbf{n}_5)$  is the population vector of the previous October, meaning the population at the onset of reproduction.
- $\mathbf{m}$  is the average number of eggs per nest.
- The quantity of chicks coming from eggs that began to be incubated in the  $i$ th decade of the incubation period is:

$$\mathbf{b}_i = \prod_{i=1}^8 \mathbf{g}_i \cdot \mathbf{h}_i \cdot \mathbf{d}_i \cdot \mathbf{e}_i \cdot \mathbf{m} \cdot \langle \mathbf{R}, \mathbf{N}(\mathbf{t}) \rangle$$

where  $e_i = e(i) \cdot e(i+1) \cdot e(i+2) \cdot e(i+3)$  corresponds to a hatching period. The individuals that are counted for the first time in the population in April are those coming from eggs that began to be incubated in the first five decades of the season of incubation and that have survived until April. In other terms, they are  $(b_1 + b_2 + b_3 + b_4 + b_5)s_a$ , where  $s_a$  is the probability of surviving from age three months until the month of April, while those coming from eggs that began to be incubated in the last four decades of the incubation season and that survive until July will be counted for the first time in July. They are  $(b_6 + b_7 + b_8 + b_9) \cdot s_j$  where  $s_j$  is the probability of surviving from age three months to the month of July. Taking into account the previous facts, the coefficients of the breeding matrices have been defined as:

$$\rho_k = \mathbf{m} \cdot \mathbf{r}_k \prod_{i=1}^8 \mathbf{g}_i \sum_{i=1}^5 \mathbf{h}_i \cdot \mathbf{d}_i \cdot \mathbf{e}_i$$

$$\varrho_k = \mathbf{m} \cdot \mathbf{r}_k \prod_{i=1}^8 \mathbf{g}_i \sum_{i=6}^9 \mathbf{h}_i \cdot \mathbf{d}_i \cdot \mathbf{e}_i$$

where  $k = 1, \dots, 5$ .



to harvest the population according to the vector  $(\lambda - 1)\nu_\lambda$  between reproduction periods while maintaining its structure and returning to its initial size. Harvesting does not occur during the breeding period.

With the purpose of including the harvest in the model a diagonal nonnegative matrix  $\Gamma$  has been built. Its components are the proportion of individuals in each stage that remain in the population after the harvest (Beddington and Taylor [1973], Doubleday [1975]).

If the harvest is carried out immediately before the census, then the remaining population will be:  $N(t+1) = \Gamma \cdot M \cdot N(t)$  and the harvested population will be:  $C(t+1) = (I - \Gamma) \cdot M \cdot N(t)$ .

Given the way in which the model has been built, it is possible to estimate the harvest in three different seasons of the year, without including the breeding season, and possible to calculate the population as well as the harvest in each one of the seasons.

For example, if the population is harvested in the period January–April:

- the harvested population is obtained by multiplying the population vector of the previous October by the matrix  $(I - \Gamma) \cdot B \cdot A$ ;
- the remaining April population is obtained by multiplying the population vector of the previous October by the matrix  $\Gamma \cdot B \cdot A$ ;
- the following October population is obtained by multiplying the population vector of the previous October by the matrix  $F = D \cdot C \cdot \Gamma \cdot B \cdot A + D \cdot C \cdot P + D \cdot \Theta$ .

### The parameters of the model.

*Coefficients of the quartile projection matrices.* The annual projection matrix contains the coefficients  $P_i$ , the probability of permanence in stage  $i$ , and  $G_i$ , the probability of growing to the next stage after one year has lapsed. With the purpose of estimating these parameters, another two which are easier to calculate are introduced:  $\gamma_i$ , the probability of growth for surviving individuals, and  $\sigma_i$ , the probability of survival.

Then, by simple conditional probability arguments the following expressions can be obtained:

$$G_i = \sigma_i \cdot \gamma_i \quad P_i = \sigma_i(1 - \gamma_i)$$



Supposing that all individuals remain for the same period  $T_i$  in the  $i$ th stage, the proportion of individuals in stage  $i$  that grows to stage  $i + 1$  in each step of time depends on the age distribution within the stage. Hence, parameter  $\gamma_i$  can be approximated by supposing that the within-stage distribution is stable, and using the iterative method cited by Caswell [1989]. Note that the approximated values yield a transition matrix whose dominant eigenvalue is close to but not necessarily equal to 1.

Assuming that the ñandú population is stable and  $\lambda = 1$ , the values of  $\sigma_i$  and  $\gamma_i$  can be estimated for this value of  $\lambda$ .

For estimating  $\sigma_i$ , an auxiliary probability  $p_j$  has been defined as the probability of survival from the  $j$ th to  $j + 1$ th year. The  $j$ th year is defined as the interval of months:  $(12.(j - 1) + 3, 12.j + 3]$ , where  $j = 1, \dots, 15$ , since the maximum recorded age is 15 years.

Then, the survival probability from one stage to the next is defined by the  $k$ th root of the product of the annual survival probabilities  $p_j$ , corresponding to the years that comprise the stage, where  $k$  is the length of stage in years. Hence, we have:

$$\begin{aligned} \sigma_1 &= p_1 \\ \sigma_2 &= p_2 \\ \sigma_3 &= p_3 \\ \sigma_4 &= (p_4 \cdot p_5 \cdots p_9)^{1/6} \\ \sigma_5 &= (p_{10} \cdot p_{11} \cdots p_{14})^{1/5} \end{aligned}$$

The probabilities  $p_j$  are computed from

$$p_j = \frac{l(j.12 + 3) + l((j + 1).12 + 3)}{l((j - 1).12 + 3) + l(j.12 + 3)}$$

where  $l(x)$  is the survival function obtained from the life table (Hutchinson [1978], Caswell [1989]). Since in our case the survivorship curve is known in the middle points of the intervals  $(12.(j - 1) + 3, 12.j + 3]$  and those points are not the ones required to calculate the values of  $p_j$ , a linear interpolation has been used.

Consider the survivorship curve in Figure 1. The coefficients of the annual matrix, which in the theoretical model was obtained as the

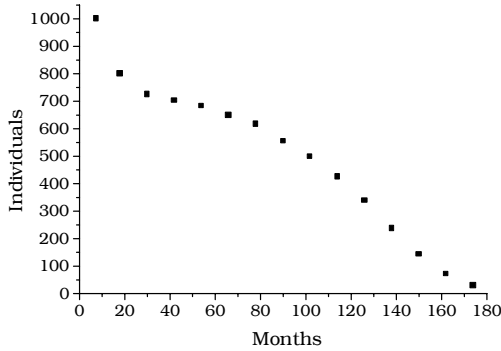


FIGURE 1. Survivorship curve for individuals older than three months.

product of four quarterly matrices, are  $P_i$  and  $G_i$ . The form of the quarterly matrices is prescribed beforehand and hence the locations of the null coefficients are known in each matrix. The others have been defined in such a way that the product of the four matrices may agree with the annual matrix.

TABLE 1. Stages considered for the population model.

STAGE	Individual's age (months)
CHAROS	(3, 15]
JUVENILE I	(15, 27]
JUVENILE II	(27, 39]
ADULTS I	(39, 123]
ADULTS II	(123, 183]

*Coefficients of the reproduction matrices  $\Theta$  and  $P$ :*

1. *Probability of nesting depending on the age.* It is known that not all individuals have the same probability of nesting and that it is strongly linked to age. As this information could not be found in the literature and is required by the model, we consulted with people who have good knowledge of this species. We obtained a range for these

age-specific probabilities and the middle point of the given range was taken to be the probability value. Thus the vector obtained:

$$R = (0, 0, 0.025, 0.3, 0.1).$$

2. *Probability of starting incubation in the  $i$ th decade of the breeding season.* These probabilities, shown in Table 2 and Figure 2, have been obtained in the field from the number of nests found over the period from October to December. For simplicity, we have excluded the possibility of a male building two nests during the same reproductive season.

3. *Probability of successful hatching in the  $i$ th decade,  $i = 1, 2, \dots, 9$ , of the breeding season.* The data for estimating these probabilities were obtained from the same fieldwork as the previous probability. The results are shown in Table 3 and Figure 3.

4. *Survival of chicks.* To obtain the probability of survival of chicks from birth to their third month, data from nests that were visited several times during this period have been analyzed. The survivorship curve that allows calculation of the quantity of chicks of the initial cohort that survive until day  $x$ ,  $l(x)$ , was obtained from fitting the values for the observed nests with an exponential function:

$$l(x) = 54.123 + 43.611 e^{(-x/14.734)}$$

By means of this function the probabilities of survival from the  $i$ th decade to the  $i + 1$ th were calculated as shown in Table 4 and Figure 4.

5. *The probabilities of survival from the third month until the time when individuals are counted for the first time.* These probabilities are assumed to be high, and hence they have been set to 0.95 (Milano, pers. comm.).

6. *The environmental conditions.* The function that reflects the environmental conditions has been defined as a discrete function. For each decade, this function can take one of five different values, between 0 and 1, depending on whether the decade is very dry, dry, normal, humid or very humid. Somewhat arbitrarily, the values were assigned as shown in Table 5. A better definition will be possible when more field data on this item will be available.

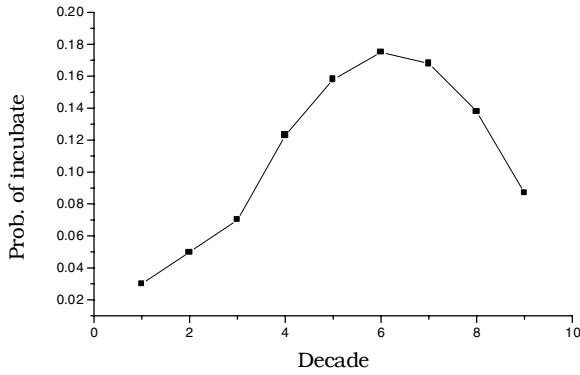


FIGURE 2. Probability of starting incubation during each of the decades of the breeding season, computed from field data.

TABLE 2. Probability of starting incubation during each of the decades of the breeding season (data from Fernández [1998] and Fernández [pers. comm.]).

Number of decades	1	2	3	4	5	6	7	8	9
Prob. of starting incubation	0.03	0.05	0.07	0.123	0.158	0.175	0.168	0.138	0.089

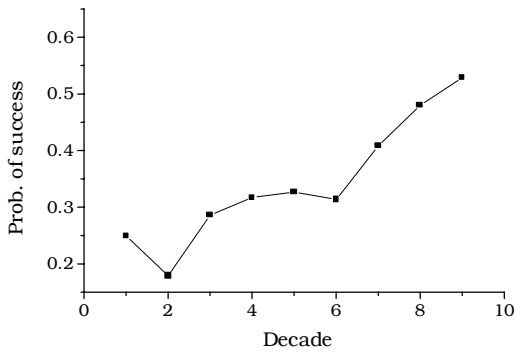


FIGURE 3. Probability of successful hatching during each of the decades of the breeding season, computed from field data.

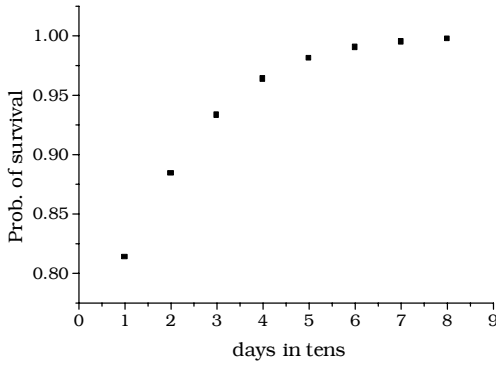


FIGURE 4. Probability of survival of chicks from birth to age three months, empirical.

TABLE 3. Probability of successful hatching for each of the decades of the breeding season (data from Fernández [1998] and Fernández [pers. comm.]).

Number of decades	1	2	3	4	5	6	7	8	9
Probability of success	0.25	0.179	0.286	0.317	0.327	0.314	0.408	0.48	0.529

TABLE 4. Probability of survival of chicks from birth to age three months (Milano [pers. comm.]).

Decade	Probability of survival from the $i$ th decade to $i + 1$ th ( $g_i$ )
1	0.81384
2	0.88396
3	0.93341
4	0.96381
5	0.98095
6	0.99015
7	0.99495
8	0.99743

TABLE 5. Function that reflects the environmental conditions.

Characteristic of Decade	Very Dry	Dry	Normal	Humid	Very Humid
Value assigned	0.25	0.75	1	0.8	0.1

*The analysis of cases.* By these means, and using available data (Fernández and Milano, pers. comm.) the quarterly matrices were calculated as:

$$A = \begin{bmatrix} 0.988 & 0 & 0 & 0 & 0 \\ 0 & 0.996 & 0 & 0 & 0 \\ 0 & 0 & 0.999 & 0 & 0 \\ 0 & 0 & 0 & 0.947 & 0 \\ 0 & 0 & 0 & 0 & 0.882 \end{bmatrix}$$

$$B = \begin{bmatrix} 0.82 & 0 & 0 & 0 & 0 \\ 0.17 & 0.786 & 0 & 0 & 0 \\ 0 & 0.2 & 0.75 & 0 & 0 \\ 0 & 0 & 0.23 & 0.944 & 0 \\ 0 & 0 & 0 & 0.05 & 0.882 \end{bmatrix}$$

$$C = \begin{bmatrix} 0.15 & 0 & 0 & 0 & 0 \\ 0.835 & 0.245 & 0 & 0 & 0 \\ 0 & 0.73 & 0.2 & 0 & 0 \\ 0 & 0 & 0.77 & 0.944 & 0 \\ 0 & 0 & 0 & 0.056 & 0.882 \end{bmatrix}$$

$$D = \begin{bmatrix} 0.9 & 0 & 0 & 0 & 0 \\ 0 & 0.99 & 0 & 0 & 0 \\ 0 & 0 & 0.988 & 0 & 0 \\ 0 & 0 & 0 & 0.947 & 0 \\ 0 & 0 & 0 & 0 & 0.882 \end{bmatrix}$$

As environmental conditions are considered to affect the reproduction, different reproduction matrices  $\Theta$  and  $P$  have been obtained by taking into account different environmental conditions during the breeding season.

When the environmental conditions during the breeding season are normal, the annual projection matrix is the following:

$$M = \begin{bmatrix} 0.109 & 0 & 0.043 & 0.512 & 0.171 \\ 0.710 & 0.19 & 0.019 & 0.234 & 0.078 \\ 0.121 & 0.604 & 0.148 & 0 & 0 \\ 0 & 0.145 & 0.752 & 0.799 & 0 \\ 0 & 0 & 0.011 & 0.081 & 0.605 \end{bmatrix}.$$

In this case the dominant eigenvalue of the annual projection matrix is  $\lambda = 1.197$ . Then, the population under normal environmental conditions has an annual growth rate of about 19%, which agrees with field observations. Note that the computation of the coefficients of the quartile matrices based on the iterative method proposed by Caswell [1989] does not take into account the breeding matrices, and hence  $\lambda$  should not be expected to be equal to 1.

The right eigenvector corresponding to the dominant eigenvalue is:

$$\nu_\lambda = (0.378 \quad 0.452 \quad 0.304 \quad 0.749 \quad 0.107)'$$

Then, the stable distribution of a population of 100 individuals is given by:

$$N_0 = (19.407 \quad 22.826 \quad 15.343 \quad 37.379 \quad 5.405)'$$

Since the environmental conditions during the breeding season change every year, there will be a different annual projection matrix for each year.

Different scenarios have been considered and a stable initial population of 100 individuals has been projected as shown in Table 6. Comparing the final population given by the different scenarios with the permanently "normal" situation, we can see that in all cases the population decreases as expected. The largest decrease is when the conditions are dry for all years, in which case we may say that the younger stages show a very poor recruitment while the fourth is reduced to about 50% of the individuals of the same stage under normal conditions. In the second case, the last stage is the one that shows less difference (25%) relative to the population under normal conditions. In the third case, the stages which exhibit the largest difference (60%) when compared to the population under normal conditions are the second and the third stages.

TABLE 6. Projection of a stable initial population.

Initial population	Environmental conditions during five consecutive breeding seasons	Final population
$N_0 = \begin{pmatrix} 19.047 \\ 22.826 \\ 15.343 \\ 37.379 \\ 5.405 \end{pmatrix}$	All years were normal	$N_5 = (46.725 \ 56.001 \ 37.655 \ 91.691 \ 13.278)'$
	All years were very dry	$N_5 = ( \ 0.129 \ 0.391 \ 1.515 \ 46.189 \ 9.806)'$
	Series: very dry, very dry, dry, dry, and normal	$N_5 = (26.936 \ 21.166 \ 8.986 \ 42.884 \ 9.774)'$
	Series: humid, normal, humid, very humid, and normal	$N_5 = (36.360 \ 20.659 \ 12.956 \ 70.886 \ 11.869)'$



The harvest was analyzed in the first case, that is, under normal climatic conditions. The vector  $c = (\lambda - 1)\nu_\lambda$ , which represents the proportion of individuals of each stage that can be removed is

$$c = (0.074, 0.089, 0.06, 0.146, 0.021)'$$

Then, the harvesting matrix  $\Gamma$  is:

$$\Gamma = \begin{bmatrix} 0.926 & 0 & 0 & 0 & 0 \\ 0 & 0.911 & 0 & 0 & 0 \\ 0 & 0 & 0.940 & 0 & 0 \\ 0 & 0 & 0 & 0.854 & 0 \\ 0 & 0 & 0 & 0 & 0.979 \end{bmatrix}.$$

It is possible to harvest once a year, choosing to do this in any one season of the year. One option is to calculate how the maximum quantity of harvested individuals change as the harvest occurs in different months under the assumption of sustainable yield. It is easily seen that the month in which the harvest is carried out affects only very slightly the quantity of individuals that remain in the population as well as the quantity that is harvested. This is because harvesting occurs only during the non-breeding period. Although there are individuals that grow from one stage to another, their proportion within the stage is relatively small, hence the outcome is not significantly different.

These few examples show that this model can adapt to various situations. Once the model is well calibrated, it could be used as a basis for building a computational tool useful to a producer or landowner interested either in the conservation of the resource ñandú or in sustainably exploiting it. The model can be used for the projection of possible scenarios and for determining possible risks and beneficial actions.

**Results and conclusions.** The purpose of this work was to formulate a mathematical model that reflects the population dynamics of *Rhea* in the short term in response to environmental variations and conditions of sustainable harvest. The model has been built with the purpose of obtaining a matrix that would be suitable for annual projections, but given the characteristics of the species it was necessary to follow the population with different time steps depending on the

stage. This is why four matrices for seasonal projections and two matrices for representing reproduction under climatic constraints have been built. The model projects the population abundance throughout time, and at the same time provides information on characteristics of the population. This information—the mid-term growth rate of the population, the stable stage distribution, and the reproductive value of each class—can be calculated from the parameters of the transition matrix.

A diagonal matrix was introduced to represent the harvest. Its elements represent the proportion of individuals in each stage that remain in the population after the harvest. The model was built in such a way that the harvest can be performed in different seasons of the year and hence different strategies can be simulated. The simulations make it possible to project the population growth over several years and to evaluate the effect of different sequences of weather conditions on the abundance of *Rheas*. They provide a landowner with an estimate to help him decide the best time and right amount to harvest to ensure a sustainable yield and the conservation of this species.

The construction of a population model that includes a harvest factor is also a good tool for the systematization of data. Although some rates are not known with precision, contacts with researchers and people familiar with the species helped propose reasonable, biologically consistent values for the construction of the model. In spite of the lack of rigorous data, the output can be considered a satisfactory first approximation. Feedback to field researchers will help them in collecting new data to compute rates more accurately, with the possibility of improving the model.

Hence, this approach can be regarded as a first step towards a more precise model that would include other aspects of interest to a conservationist or a manager.

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