

## Population viability analysis of the Uruguayan Creole cattle genetic reserve

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### Summary

Uruguayan Creole cattle are descended from animals brought by the Spanish conquerors. The population grew extensively without directional management and became semi-wild before the introduction of commercial breeds in the 19th century. Today only 575 animals remain, restricted to the San Miguel National Park. We performed a population viability analysis of this reserve using VORTEX v. 8.31 to study its demographic and genetic parameters, assess the environmental factors that affect its development, evaluate its future risk of extinction and test different management options. The probability of extinction in the next 100 years was always zero, even in the more pessimistic scenarios. The growth rate of the population was always positive and mostly affected by the mortality rate of calves. Population size increased rapidly up to carrying capacity, this being the only limiting factor for population growth. Retained heterozygosity was always above 90% and the inbreeding coefficient below 0.10. The analysis shows that the population is not at risk due to its genetic diversity and demographic structure, however all the individuals are concentrated in only one place. We suggest its subdivision into sub-populations located in different regions and connected by gene flow, decreasing the risk of extinction and accomplishing the conservation and self-sustainability goals.

### Resumen

La raza vacuna Criolla uruguaya descende de los animales traídos por los conquistadores españoles. La población creció de forma extensiva sin ningún tipo de gestión y se convirtió en semi-salvaje antes de la llegada de las razas comerciales en el siglo XIX. Hoy en día sólo quedan 575 animales, principalmente concentrados en la región del Parque Nacional de San Miguel. Se realizó un análisis de viabilidad de la población en esta reserva utilizando VORTEX v.8,31 para estudiar sus parámetros demográficos y genéticos, controlar los factores ambientales que afectan su desarrollo, evaluar los riesgos futuros de extinción y probar distintas formas de gestión. La probabilidad de extinción en los próximos 100 años fue cercana a cero, incluso considerando las opciones más pesimistas. La media de crecimiento de la población fue siempre positiva y mayormente se vio afectada por la media de mortalidad de las terneras. El incremento rápido de la población para desarrollar su capacidad fue el único factor limitante para el crecimiento poblacional. La heterocigosis fue siempre por encima del 90% y el coeficiente de consanguinidad por debajo de 0,10. El análisis mostró que la población no se encuentra en peligro gracias a su diversidad genética y a la estructura demográfica, sin embargo, todos los individuos están concentrados en un único lugar. Sugerimos subdividir las subpoblaciones localizadas en distintas regiones y conectarlas por un flujo de genes,

para de esta manera disminuir el riesgo de extinción y llevar a cabo un programa de conservación con objetivos de auto sostenibilidad.

**Keywords:** *Population viability analysis, Uruguayan Creole cattle, modelling, Carrying capacity of the environment, Population Viability Analysis (PVA).*

## Introduction

Local cattle populations have a very valuable genetic potential for sustainable agriculture, as they represent the consequence of local adaptation processes. Unlike commercial breeds, strongly selected for production purposes, local breeds have evolved mostly as a result of natural selection for centuries, becoming a very interesting source of genetic variation. They are a key factor for promoting sustainable development together with environmental preservation (Cardellino, 2002; derived from FAO, 1998).

In Latin America many animal genetic resources are at risk, mainly due to the process of genetic introgression from commercial breeds (Medrano, 2000). Most local breeds persist as small, scattered populations. Small populations are unstable, as they are more exposed to the random fluctuations of factors that can lead to extinction, such as demographic stochasticity, environmental variation, catastrophes, genetic drift and inbreeding depression. The combination of these random forces destabilizes small populations, in a feedback process called the "extinction vortex" (Ballou, 1993; Lacy and Clark, 1993).

Several approaches can be used to assess the risk of extinction of small populations, Population Viability Analysis (PVA) being the most widely applied. PVAs are computer models that allow population managers to simulate the dynamics of the extinction process, estimate the effects of the interacting random factors and assess the long-term viability of small populations. They provide quantitative predictions for population

growth, demographic fluctuations and genetic variation, based on different assumptions. PVAs are also useful for testing the adequacy of alternative management options (Lindenmayer *et al.*, 1993; Lacy and Clark, 1993). Several PVA packages have been proposed (Brook *et al.*, 1999).

As an example of American Creole cattle, the Uruguayan Creole descends from the cattle brought by the Spanish conquerors after their discovery of Uruguay in 1492. The first bovines were introduced to what is now Uruguay between 1611 and 1620, from the Iberian Peninsula and the Jesuit Missions of Alto Uruguay (Primo, 1992). The extremely good environmental conditions for these animals favoured their multiplication in the region. The cattle population grew extensively, without directional management and became semi-wild. Late in the 19th century, the introduction of more selected European breeds caused the decline of the Creole cattle (Giovambattista *et al.*, 2001).

After 400 years of natural selection, Uruguayan Creole cattle (UCC) are considered to be adapted to the environment of the country. Even considering the possibility of some genetic introgression from commercial breeds, it is assumed that they have remained mostly in reproductive isolation, as their phenotype is clearly similar to other American Creole cattle and to certain Spanish ancient breeds considered ancestral (Postiglioni *et al.*, 1998; Rincón *et al.*, 2000; Rodríguez *et al.*, 2001). Today there are only around 600 animals restricted to San Miguel National Park, in the department of Rocha in the south-east of Uruguay. This reserve originated from a foundation stock of 35 individuals that were brought from inhabited regions of the country in around 1930 (Arredondo, 1958). These animals were the remnants of the original huge population that spread over all the country, and had lived under natural, unmanaged conditions until that moment.

The reserve consists of 25 bulls, 445 cows and 105 calves of both sexes, in an area of 600 hectares of wetlands, prairies, native woods and ridges. Directional management

of the population is minimal, consisting only of the periodic extraction of a certain number of males as a way of controlling population size. Mating occurs in natural conditions and the reserve has never been subject to any kind of artificial selection.

The objective of this study was to perform a population viability analysis of the present San Miguel Creole cattle reserve, to study its demographic and genetic parameters and to assess the environmental factors that may affect its development. We also evaluated the risk of extinction and test different management options.

## Materials and Methods

The complex interactions between demographic, environmental and genetic factors in the UCC population were examined by computer simulation modelling using the program VORTEX, version 8.31. The structure, algorithms and assumptions of the program are outlined in Lacy (1993). VORTEX is a population viability assessment program for modelling population dynamics. It allows for the variation of levels of different parameters and management options, and estimates their effects on the population, this being an aid to conservation goals. The model has been widely used in several species and is especially powerful for modelling vertebrate wildlife population behaviour (Lacy, 1993; Lacy and Clark, 1993). This is the first time this program will be used to analyze the dynamics of a semi-wild population of a domestic species.

The program yields the following information:

- The probability of persistence of the population: for a maximum population size ( $N_{max}$ ) the expected persistence time will depend on the average growth rate  $r$  ( $r = \text{no. births} - \text{no. deaths}$ ) as well as the variance of this parameter due to environmental fluctuations.
- The size of the average population along the time scope considered.

- The expected and observed retained average heterozygosity after the time scope considered.

VORTEX simulates the transmission of alleles from parents to offspring at a hypothetical neutral (non-selected) genetic locus, and so models the loss of genetic diversity. At the beginning of the simulation each animal is assigned two unique alleles for that locus, and each offspring created during the simulation is assigned one of the alleles from each parent at random. VORTEX assesses how many of the original alleles remain in the population, and the average heterozygosity (gene diversity) relative to the starting levels (Lacy, 1993). VORTEX can indicate the average number of alleles, the final allele composition of the population, the growth rate (stochastic and deterministic  $r$ ) and the probability of extinction: in VORTEX extinction is defined as the absence of any of the sexes.

The variables introduced were:

- The size of the initial population: two basic scenarios were performed considering two initial population sizes, one with the present population size of 575 animals, and another one with an alternative smaller population size of 400 tested as a management option. Age and sex distribution were the same as in the present real population, derived from the census data of the year 2002 (Table 1). For the 400 individual population, age and sex classes were calculated in proportion to the real distribution. During simulations VORTEX distributed the age-sex structure according to the reproduction and death rates specified in each scenario, using the deterministic algorithms of Leslie's matrix.
- The number of iterations and years (time scope): every scenario was repeated 100 times and for 100 years. Results were summarized every ten years.
- The carrying capacity of the environment ( $K$ ): two basic scenarios were considered, one with a  $K$  of 600 (s.d. 50) individuals, similar to the real estimate for an area of 600 hectares in this geographical region,

Table 1. Age and sex distribution of the UCC founder (c. 1930) and present (2002) populations.

Age and sex class	Founder population (N = 35)	Present population (N = 575)
Females 0 -1 years	4	50
Females 1 - 2 years	-	90
Females 2 - 3 years	-	125
Females 3 years or more	25	230
Males 0 - 2 years	4	55
Males 2 years or more	2	25

and another one of 1 000 (s.d. 80) individuals, to test the growth potential of the population. VORTEX fixes carrying capacity as an upper limit for population size, beyond which an additional mortality rate is imposed, proportional along all age-sex classes in order to return the population to the specified K value.

- Migration and supplementation: these were not considered, as this is the only known UCC population.
- The mating system: the breeding system modelled by VORTEX assumes that mates are randomly reshuffled each year and that all animals that can breed have an equal probability of breeding. It is possible to choose between monogamous mating, where there must be a male for each female, or polygamous mating, where there needs to be at least one breeding male for all breeding females. The UCC has polygamous mating.
- The age of reproductive maturity of females: one year (not considering gestation period). The age of reproductive maturity of males is two years.
- The maximum breeding age (senescence): nine years, for both sexes.
- The sex ratio at birth: 50%.
- The average litter size: one.
- The proportion of adult females and males in the breeding pool: the proportion of breeding females per year is 55% (s.d.: 10%). Three different scenarios were studied according to a proportion of breeding males of 15%, 30% and 50%, 15% being the approximate present value

and 50% an ideal natural scenario. The value of 30% is an intermediate alternative management option.

- Inbreeding depression: we have not detected in the population the effects of inbreeding depression, as the estimated values for inbreeding based on recent studies of this reserve with molecular markers show a very low inbreeding coefficient of between 0.020 and 0.038 (Postiglioni *et al.*, 1998; Armstrong, 2004).

However, we wanted to test if inbreeding could be a future problem. In VORTEX inbreeding depression is modelled as a loss of viability of inbred animals during their first year. The severity of inbreeding depression is measured by the number of "lethal equivalents", this being an estimate of the average number of lethal alleles per individual in the population if all deleterious effects of inbreeding were caused only by recessive lethal alleles (Lacy, 1993). In this case we assumed that the studied species responded to inbreeding in a similar way to the average (3.14 lethal equivalents per diploid genome) reported in the survey of 40 ungulate mammal species by Ralls *et al.* (1988).

- Reproduction and survival: as these cattle live in a natural environment, survival and reproduction are related. Being a domestic species subjected to certain management practices, reproduction does not depend on population density but only on the carrying capacity of the environment.
- Mortality: mortality can be introduced into VORTEX in four different ways:



- a) as the annual expected mortality rate for each age-sex class, with its corresponding standard deviation;
  - b) as a fixed number of harvesting (extractions) of animals for each age-sex class;
  - c) as a catastrophic event that reduces the normal survival rate to a fixed amount; and
  - d) when K is exceeded all age-sex classes are proportionally reduced, as was said before.
- Three different scenarios for the annual mortality rate of individuals under one year of age (calves of both sexes) were considered: 10% (s.d. = 3%) similar to the current estimations, 25% (s.d.=5%) as an intermediate value, and 40% (s.d.=5%) as a maximum value related to environmental conditions, the first year of life being most critical in large mammals. The annual mortality rate of animals above one year of age is 3% (s.d.=0.8%). The harvesting of males was also considered, as this is a current practice in the reserve. Three different possibilities were explored in the analysis: 0 (no harvesting), 25 and 50 animals per year. Today around 50 young bulls of one year of age are harvested every year, as a way of controlling the population size.

Catastrophes are events that affect the population beyond the normal parameters of environmental variation, defined by VORTEX as an increase in adult mortality. They can affect reproduction, survival or both. Examples are severe food shortage, floods, fires, droughts or epidemics. Catastrophic events are introduced with a probability of occurrence and a severity factor of between 0.0 (maximum effect) and 1.0 (no effect). We considered a probability of 5% per year (one every 20 years), affecting the reproduction of 50% of the animals and the survival of 20% (0.5 and 0.2 severity factor, respectively).

In order to analyze how this reserve could have developed, two simulations were performed taking into account the foundation population from which this

reserve originated. It consisted of 35 individuals, of known sex and age according to historical data from Arredondo (1958) (Table 1). The simulations were performed for a time scope of 70 years (1930-2000) under similar conditions to those naturally experienced by for cattle species (50% of reproductive males, 65% of reproductive females and 25% of annual mortality rate of individuals under one year of age). The other parameters were observed in the same way as in the previously cited simulations. The only variable parameter introduced in this case is male harvesting (as it is not known how the population was managed in this respect) using one scenario with no harvesting and another with the harvesting of 40 males per year starting from the tenth year.

In the present and foundation populations there is a clear predominance of reproductive females above three years of age. The ratio of males and females has been maintained relatively constantly throughout the history of the population. In the present reserve, males represent 14% of the total population, and constituted 17% of the foundation population. With reference only to the reproductive males, they represent 6.6% of the current population represented 7.4% of the foundation population.

## Results. Population Viability Analysis (PVA)

The results of the Population Viability Analysis (PVA) are shown in the Appendix. In total, 100 simulations of 83 different scenarios were performed. The probability of extinction of the population in 100 years was always zero, even in the more pessimistic scenarios with a mortality rate of individuals under one year of age of 40%, only 15% of males in the breeding pool and the harvest of 50 males per year.

In all cases the population size increased rapidly until maximum carrying capacity is reached, in less than ten years (Figure 1). The

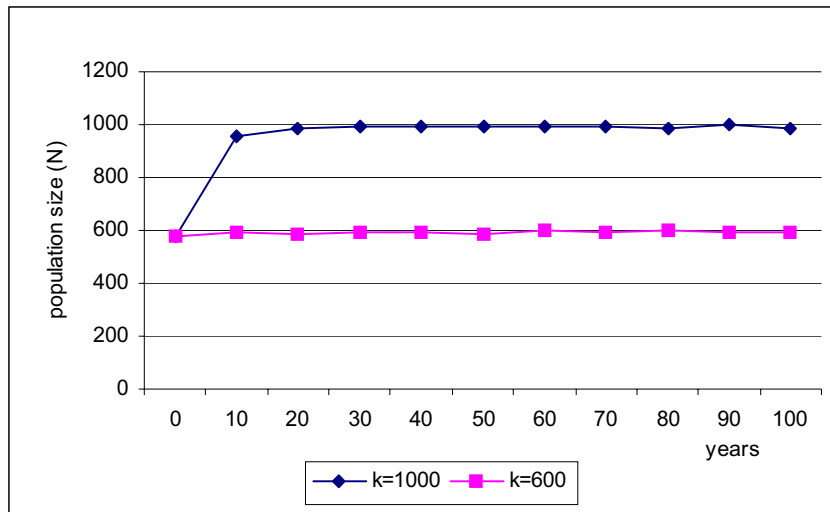


Figure 1. Population size vs. time, according to carrying capacity and for the next 100 years, taking as start point scenario the present one (population of 575 animals, 10% mortality rate of calves, 15% of reproductive males and harvest of 50 males per year).

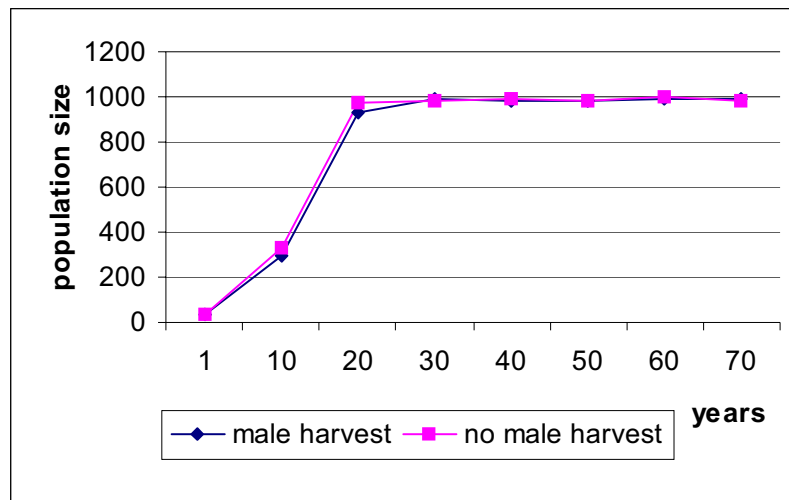


Figure 2. Population size vs. time for different male harvest strategies, taking as start point scenario the founder population of 35 individuals (Arredondo, 1958).

same happens when the growth of the foundation population of 35 individuals is simulated (Figure 2). According to this, the carrying capacity would be the only limiting factor for population growth. Today it can be observed that the population is in constant growth, the annual harvest of males being

the only means to avoid exceeding the carrying capacity of the area designated for the reserve.

In our analysis the observed growth rate ( $r$ ) of the population was always positive, and was mostly affected by the mortality rate of individuals under one year of age, decreasing as this rate increased (Figure 3).

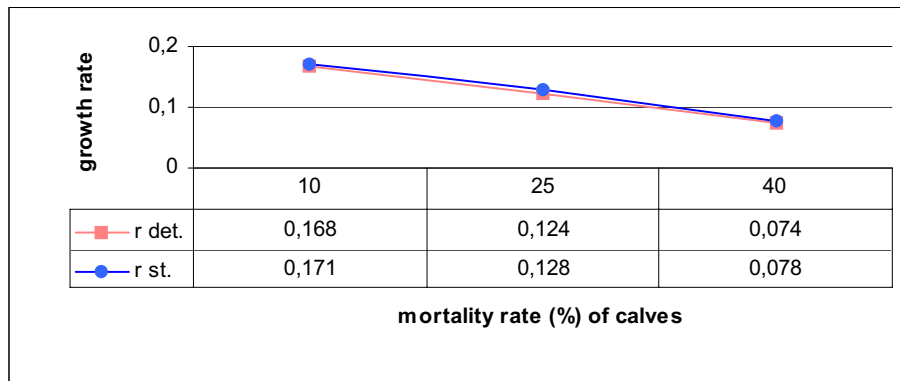


Figure 3. Growth rate (*r*) vs. mortality rate of calves. The start point scenario is the present population, with 15% of reproductive males and harvest of 50 males per year. *r det.*: deterministic *r*; *r st.*: stochastic *r*.

The values of retained genetic diversity were very high, even in the most pessimistic scenarios, which is a key factor for conservation strategies. Remaining heterozygosity was always above 90% and the inbreeding coefficient was below 0.10. This shows that the age-sex distribution of the population allows for adequate levels of genetic diversity to be maintained along time.

The proportion of reproductive males did not affect the predicted level of genetic diversity retained after 100 years. Although an increase in the retained heterozygosity and a decrease in the inbreeding coefficient could be observed as the proportion of reproductive males increased, these differences were not relevant (Table 2). The harvest of males had even less effect on this parameter.

These results clearly show that the population is able to survive and develop with the current age-sex classes and genetic

diversity, and that it is most significantly subject to geographic area availability.

## Discussion

The analysis performed with VORTEX clearly showed that the population is not at risk due to intrinsic factors, such as genetic diversity and demographic structure. Very high predicted levels of retained heterozygosity could be observed after 100 years of simulations, without a significant increase in inbreeding. According to Ballou (1993), a management program that predicts a probability of 95% of population survival and a 90% of retained genetic diversity for the next 100 years can be considered successful.

Several studies with molecular markers of the UCC population, including the analysis of 18 microsatellites, revealed high levels of

Table 2. Levels of inbreeding and of retained heterozygosity for the next 100 years for different percentages of reproductive males. The start point scenario is the present population (575 animals, carrying capacity: 600, 10% of mortality of calves and harvest of 50 males per year).

% of males	F	He
15	0.067	0.9311
30	0.052	0.9476
50	0.039	0.9570



*Figure 4. A herd of Uruguayan Creole cattle.*



*Figure 5. Example of genetic diversity in a herd of Uruguayan Creole cattle.*

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observed heterozygosity ( $>0.50$ ) and low levels of inbreeding ( $<0.05$ ) (Rincón *et al.*, 2000; Postiglioni *et al.*, 2002; Armstrong, 2004; Armstrong *et al.*, 2005). All these findings suggest that the demographic structure of the population is stable and able to maintain good levels of genetic diversity through time, given the current management strategies (Figure 4 and 5).

The parameters obtained showed that the population is safe from the genetic and demographic factors for the next 100 years. In all the simulations we obtained positive values of  $r$ , which shows that the population has a very high intrinsic growth potential. The clear predominance of reproductive females above three years of age, in the present and in the foundation populations, must have favoured the development of the population at the outset as well as in its current growth. The carrying capacity of the environment is the only limiting factor. It is clear that the reserve could grow and develop without reaching risky inbreeding levels if it had better opportunities for expansion. This could be achieved, for example, by increasing the available geographical area.

According to Lacy (1993) and Foose (1993), in order to minimize the consequences of genetic drift and founder effect, small managed populations should start with a number of founders not less than 20 and reach the carrying capacity of the environment as soon as possible. It is estimated that 20 founders would carry approximately 97.5% of the genetic variability present in the ancestral population and the rate of genetic diversity loss would be 2.5% per generation as the population grew. A final effective population size ( $N_e$ ) of 100 individuals would serve to retain at least 90% of its genetic diversity. So, the carrying capacity of the environment should be significantly larger than the  $N_e$  if this objective is to be accomplished. In the case of the UCC reserve, which is descended from 35 founder animals, population development has been rapid. Today the reserve consists of 575 individuals, the  $N_e$

estimated is 87, and the carrying capacity of the area is estimated at 600 animals. These data show that the population is in an acceptable situation for the conservation of its genetic diversity, but an increase in size and carrying capacity of the environment would be better for its continued development.

The mortality of animals of less than one year of age is the internal factor that affects the population growth most noticeably. It is important however, to maintain low rates of calf mortality if a rapid expansion of the population is required for management reasons. According to field data from the last two years, the actual rate is around 10%. In the present analysis it is showed that this percentage is adequate for maintaining a high population growth rate.

According to the predictions of the simulations, the proportion of breeding males and the harvest of males do not have an important effect on population growth or on the genetic diversity levels retained. This means that the reserve could be maintained with the current percentage of only 15% of males in the breeding pool, which makes management easier. In the case of an annual rotation of males being performed, high levels of genetic diversity would be maintained, but the subsequent increase in heterozygotic frequency would alter the genetic parameters of the population. On the other hand, the low proportion of breeding males in comparison to the females diminishes significantly the  $N_e$  and can cause a bottleneck effect (Hartl, 1988; Kantanen *et al.*, 2000).

The risk degree of a breed depends on many factors. According to FAO (derived from FAO, 1998) and Ponzoni (1997), the UCC can be considered as threatened, taking into account the relative number of breeding males and females. However, there are other criteria for the evaluation of the risk level of a breed or population that take into account levels of genetic diversity, demographic indexes, geographical localization of the populations, number of founders, etc. (da Gama, 2002; Lacy, 1993).

In the present situation, the UCC is not at risk in relation to its genetic and demographic parameters. However, the fact that all the Uruguayan Creole cattle are concentrated in only one location places the reserve in a potentially hazardous situation. If the population suffered from extreme local conditions or catastrophe, such as a severe draught, flood or some infectious disease, that led the population to a critical minimum number, it might not be able to recover and the UCC could disappear completely.

### Management implications

The PVA allowed us to identify and quantify the actual trends in the population under the present circumstances. Modelling population dynamics provides a prediction of the likely behaviour of populations in response to selected parameters, and is also useful in determining key management measures.

Further use of PVA to test different possible scenarios could help to develop other management measures, for example, the regulation of population size by means of harvesting both males and females in order to assure the viability and maintenance of an adequate  $N_e$  and genetic variability.

We suggest an alternative management strategy to lower the potential risk of concentrating the population in a unique geographical area, applying a metapopulation model (Ballou, 1993; Lacy, 1993). The present population has enough levels of genetic diversity and potential growth to allow its subdivision into many sub-populations without putting at risk the future of the breed. This is an important advantage in conservation as it allows for better planning and more effective management (Lacy and Clark, 1993; Lindenmayer *et al.*, 1993).

These sub-populations would be located in different regions of the country, avoiding the risk of extinction associated with a given local extreme circumstance. When the management option allowed it, they would be connected by gene flow, by the exchange

of breeding individuals. This system favours the maintenance of high allelic diversity and increases considerably the effective population size. High rates of migration contribute to the stability of the sub-populations and reduce the risk of extinction (Ballou, 1993; Lacy, 1993).

This model would allow for the maintenance of genetic reserves in San Miguel National Park and in other natural areas and for the evaluation of productive parameters in the natural environment without any artificial selection (*in-situ* conservation). We also propose the creation of other sub-populations with different environmental and management situations, including some kind of artificial selection in order to evaluate the productivity and viability of the UCC for its sustainable use.

The implementation of a more accurate system of individual identification and a pedigree register of the population would be of invaluable aid for its management. A germplasm bank of semen and embryos is also important for the conservation of the breed, as it allows for a wider scope of future management options.

In this way, the extinction risk of the UCC would be decreased, accomplishing the conservation and self-sustainability goals.

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## Appendix

Population viability analysis for the 83 scenarios. Scenario (Sc.), % mortality of individuals of less than 1 year of age (mort 0-1), % of males in the breeding pool (% males), number of males harvested per year (male harv.), deterministic  $r$  (det  $r$ ), stochastic  $r$  (st.  $r$ ), proportion of retained observed (Ho) and expected (He) heterozygosity after the time scope considered, inbreeding coefficient attained after the time scope considered (F) and probability of extinction of the population (Ext. P).

Initial population size: 400, carrying capacity: 600.

Sc.	Mort 0-1	% males	Male harv.	Det. $r$	St. $r$	Ho	He	F	Ext. P
1	10	15	50	0.168	0.1710	0.9415	0.9386	0.059	0
2	25	15	50	0.124	0.1281	0.9425	0.9406	0.058	0
3	40	15	50	0.074	0.0783	0.9432	0.9406	0.057	0
4	10	30	50	0.168	0.1712	0.9563	0.9525	0.043	0
5	25	30	50	0.124	0.1286	0.9547	0.9546	0.045	0
6	40	30	50	0.074	0.0789	0.9590	0.9552	0.041	0
7	10	50	50	0.168	0.1712	0.9586	0.9578	0.041	0
8	25	50	50	0.124	0.1278	0.9619	0.9597	0.038	0
9	40	50	50	0.074	0.0777	0.9625	0.9606	0.038	0
10	10	15	25	0.168	0.1730	0.9417	0.9399	0.058	0
11	25	15	25	0.124	0.1286	0.9472	0.9429	0.053	0
12	40	15	25	0.074	0.0800	0.9518	0.9509	0.048	0
13	10	30	25	0.168	0.1727	0.9588	0.9559	0.041	0
14	25	30	25	0.124	0.1287	0.9606	0.9574	0.039	0
15	40	30	25	0.074	0.0795	0.9635	0.9601	0.037	0
16	10	50	25	0.168	0.1712	0.9638	0.9612	0.036	0
17	25	50	25	0.124	0.1287	0.9651	0.9636	0.035	0
18	40	50	25	0.074	0.0796	0.9674	0.9642	0.033	0
19	10	15	0	0.168	0.1741	0.9477	0.9451	0.052	0
20	25	15	0	0.124	0.1305	0.9496	0.9467	0.050	0
21	40	15	0	0.074	0.0819	0.9565	0.9526	0.044	0
22	10	30	0	0.168	0.1738	0.9596	0.9567	0.040	0
23	25	30	0	0.124	0.1303	0.9638	0.9611	0.036	0
24	40	30	0	0.074	0.0803	0.9640	0.962	0.036	0
25	10	50	0	0.168	0.1735	0.9636	0.9621	0.037	0
26	25	50	0	0.124	0.1299	0.9669	0.9647	0.033	0
27	40	50	0	0.074	0.0806	0.9689	0.9664	0.031	0

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Initial population size: 575, carrying capacity: 600.

Sc.	Mort 0-1	% males	Male harv.	Det. r	St. r	Ho	He	F	Ext. P
28	10	15	50	0.168	0.1706	0.9331	0.9311	0.067	0
29	25	15	50	0.124	0.1264	0.9357	0.9321	0.064	0
30	40	15	50	0.074	0.0770	0.9320	0.9285	0.068	0
31	10	30	50	0.168	0.1711	0.9485	0.9476	0.052	0
32	25	30	50	0.124	0.1265	0.9519	0.9491	0.048	0
33	40	30	50	0.074	0.0764	0.9487	0.9451	0.051	0
34	10	50	50	0.168	0.1716	0.9597	0.9570	0.039	0
35	25	50	50	0.124	0.1266	0.9575	0.9563	0.043	0
36	40	50	50	0.074	0.0772	0.9542	0.9518	0.046	0
37	10	15	25	0.168	0.1726	0.9440	0.9407	0.056	0
38	25	15	25	0.124	0.1274	0.9460	0.9426	0.054	0
39	40	15	25	0.074	0.0792	0.9499	0.9469	0.050	0
40	10	30	25	0.168	0.1723	0.9578	0.9547	0.042	0
41	25	30	25	0.124	0.1300	0.9603	0.9572	0.040	0
42	40	30	25	0.074	0.0780	0.9610	0.9581	0.039	0
43	10	50	25	0.168	0.1724	0.9646	0.9618	0.035	0
44	25	50	25	0.124	0.1280	0.9652	0.9624	0.035	0
45	40	50	25	0.074	0.0795	0.9668	0.9642	0.034	0
46	10	15	0	0.168	0.1729	0.9486	0.9465	0.051	0
47	25	15	0	0.124	0.1295	0.9521	0.9501	0.048	0
48	40	15	0	0.074	0.0821	0.9587	0.9552	0.041	0
49	10	30	0	0.168	0.1737	0.9619	0.9581	0.038	0
50	25	30	0	0.124	0.1316	0.9625	0.9599	0.038	0
51	40	30	0	0.074	0.0812	0.9676	0.9638	0.033	0
52	10	50	0	0.168	0.1753	0.9640	0.9625	0.036	0
53	25	50	0	0.124	0.1308	0.9662	0.9653	0.034	0
54	40	50	0	0.074	0.0814	0.9694	0.9672	0.030	0

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Initial population size: 575, carrying capacity: 1000.

Sc.	Mort 0-1	% males	Male harv.	Det. r	St. r	Ho	He	F	Ext. P
55	10	15	50	0.168	0.1714	0.964	0.9623	0.036	0
56	25	15	50	0.124	0.1287	0.9648	0.9634	0.035	0
57	40	15	50	0.074	0.0790	0.9681	0.9654	0.032	0
58	10	30	50	0.168	0.1716	0.9736	0.9718	0.026	0
59	25	30	50	0.124	0.1282	0.9755	0.9732	0.024	0
60	40	30	50	0.074	0.0785	0.9755	0.9742	0.024	0
61	10	50	50	0.168	0.1722	0.9765	0.9753	0.023	0
62	25	50	50	0.124	0.1288	0.9774	0.9768	0.022	0
63	40	50	50	0.074	0.0783	0.9789	0.9768	0.021	0
64	10	15	25	0.168	0.1726	0.9651	0.9632	0.035	0
65	25	15	25	0.124	0.1298	0.9689	0.9663	0.031	0
66	40	15	25	0.074	0.0802	0.9682	0.9684	0.031	0
67	10	30	25	0.168	0.1731	0.9742	0.9731	0.026	0
68	25	30	25	0.124	0.1292	0.9761	0.9744	0.024	0
69	40	30	25	0.074	0.0809	0.9774	0.9758	0.022	0
70	10	50	25	0.168	0.1728	0.9786	0.9767	0.021	0
71	25	50	25	0.124	0.1291	0.9792	0.9775	0.020	0
72	40	50	25	0.074	0.0808	0.9806	0.9787	0.019	0
73	10	15	0	0.168	0.1737	0.9683	0.9655	0.032	0
74	25	15	0	0.124	0.1298	0.9686	0.9677	0.032	0
75	40	15	0	0.074	0.0819	0.9716	0.9703	0.029	0
76	10	30	0	0.168	0.1748	0.9750	0.9738	0.025	0
77	25	30	0	0.124	0.1310	0.9771	0.9754	0.023	0
78	40	30	0	0.074	0.0820	0.9790	0.9769	0.021	0
79	10	50	0	0.168	0.1737	0.9797	0.9778	0.020	0
80	25	50	0	0.124	0.1303	0.9798	0.9783	0.019	0
81	40	50	0	0.074	0.0817	0.9808	0.9793	0.019	0

Founder population. Population size: 35, carrying capacity: 1000.

Sc.	Mort 0-1	% males	Male harv.	Det. r	St. r	Ho	He	F	Ext. P
82	25	50	40	0.165	0.1705	0.9400	0.9393	0.060	0
83	25	50	0	0.165	0.1730	0.9443	0.9427	0.056	0

