

MODELLING THE DYNAMICS AND MANAGEMENT OF IBEX POPULATIONS IN SWITZERLAND¹.

Hirzel A.H.*, Perrin N.*

* *Institute of Zoology and Animal Ecology, University of Lausanne, CH-1015, Switzerland.*

Abstract

The IBEX (*Capra ibex*) was reintroduced in Switzerland in 1906, and then given a protected-species status. Since then its numbers have grown rapidly, and are now becoming excessive, as attested by heavy damages to the environment in certain areas, competition with the CHAMOIS (*Rupicapra rupicapra*) and the appearance of epidemics. For this reason, some culling was authorised in the 1980s, but this has been conducted purely on the basis of empirical data. Our objective is to develop culling strategies on more rational grounds. Due to its biological peculiarities and protected status, the Ibex seems particularly suitable for this approach, especially with respect to the quality of statistical data available.

How many animals to cull, and of which sex, age or populations ? To answer such questions we are developing a computer model designed to test various options. The preliminary version (*Sim-Ibex 1.1*) estimates, on the basis of the statistics available for each colony, the dependence of the fecundity and survival on the age and density in each population, as well as the magnitude of environmental stochasticity. On this basis, it then provides simulations of local population dynamics, and finally proposes and tests locally-adapted culling strategies. This version is user-friendly enough to be used directly by fauna managers.

The next steps in our work will consist of refining the parameters of the model and extending it in order to include the effects of the spatial structure of colonies and migrations between them. Finally we shall examine the possibilities of extending the software to other ungulate species.

Key words : *Capra ibex*, modelisation, population dynamic, fauna management

Introduction

Paleontological studies attest the presence of the Ibex (*Capra ibex*) in Switzerland since prehistorical times. Between the XVI th and XVIII th century, man exterminated almost all the Alps colonies. In Italy only survived a small livestock in the Gran Paradiso region, protected in the hunting territory of the kings.

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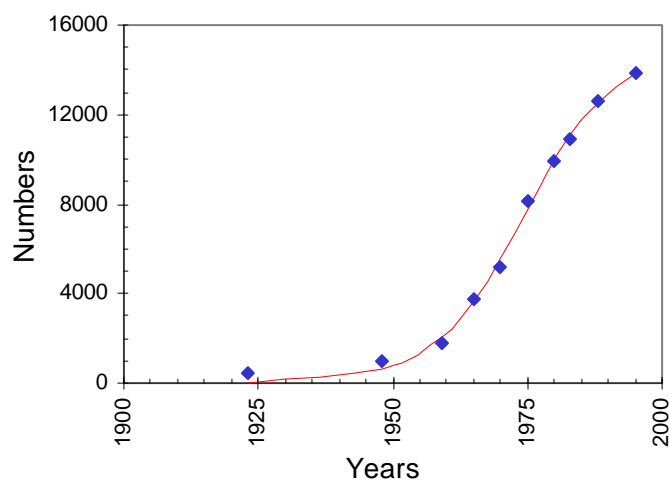


Fig. 1 : Since its reintroduction in Switzerland, the Ibex numbers have grown rapidly following a logistical curve (line). ($r = 0.12$, $K = 15'000$, $R^2 > 0.99$)

After many tries the Ibex was successfully reintroduced in Switzerland in 1911. It was then given a protected-species status. Since then, its numbers have grown rapidly (Fig. 1), and are now becoming excessive; the overpopulation involves many negative effects : heavy damages to meadows and trees, health problems due to the lack of food and to stress, appearance of diseases (e.g. pneumonia, parasitism, kerato-conjunctivitis, scab), competition with Chamois (*Rupicapra rupicapra*) (ORB, 1991).

In a first attempt to reduce local densities, since 1938, Ibexes were captured and dispatched to other places ; but this method was insufficient to stabilise the numbers at an acceptable level, so in 1977 the Swiss government authorised a regulation culling ; until now it has been conducted purely on empirical grounds. As other Swiss ungulates are over abundant too, this prompted us to develop a theoretical model to understand their dynamics and how to regulate them.

The Ibex presents several characteristics that make it particularly suitable for such a theoretical approach :

- 1° Since its reintroduction each of its colonies has been attentively followed by biologists ; field studies have collected a great amount of data about its numbers and life history ; particularly, since 1991, the census of each colony is yearly taken by age and sex classes ; this is possible owing to the following biological and ecological peculiarities.
- 2° Ibex mountain habitat, above the forest limit, makes the census easier to conduct so that statistical data are more reliable than those of other ungulates.
- 3° Male horns permit to evaluate their age without capturing them.
- 4° Each colony - living at the top of mountains - is at first approximation isolated from its neighbours, so we can treat it as a closed system.
- 5° Its status of protected species gives us long time series of data with colonies evolving according to a natural dynamic (i.e., without hunt).

The model

The survival rates of Ibexes allow to distinguish three phases, hereafter referred to as *young*, *adult* and *old* (Fig. 2). Class boundaries depend on sex, the males having a lower longevity. However, survival rates within classes are the same. Finally female fecundity is assumed constant from the age of three years (younger females have a zero fecundity).

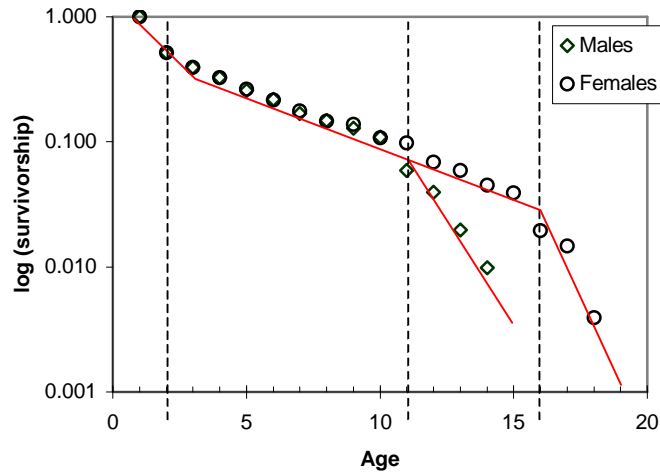


Fig. 2 : Survivorship curve for the Ibex males (squares) and females (circles). This is a type I curve with higher mortality at the end of the life. The males have a shorter life than females. For each sex, the life seems to be divided in three phases according to their survival rates : young and old one have a lower survival (~ 0.5) than adults (~ 0.7). The eye-drawn lines show the survival rate of the three age classes. (Derived from ORB (1991), fig. 4)

This life history can be modelled through two interconnected age-structured Leslie's matrices, one for each sex. The time unit is the year ; the four coefficients are described in Fig. 3.

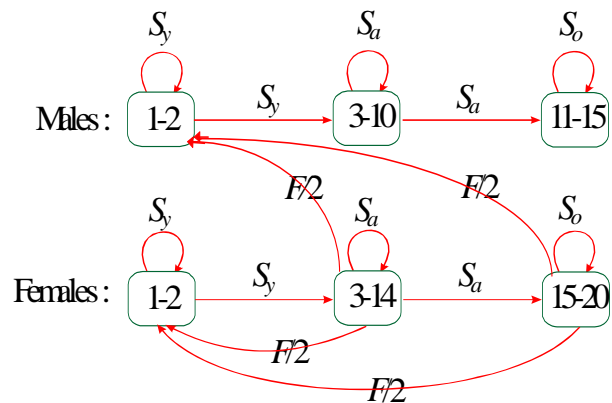
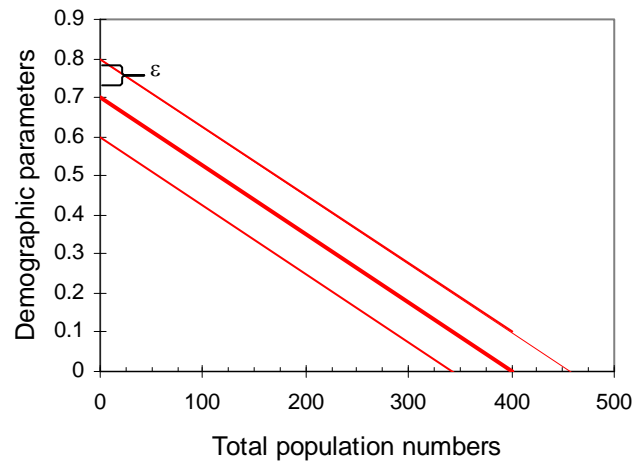


Fig. 3 : The model is based on three age classes (young, adult and old) distinguished according to survival (S_{xy}) and fecundity (F) : Female fecundity is zero up to the age of three years, then constant for all ages. The birth sex ratio is assumed to be 1:1.

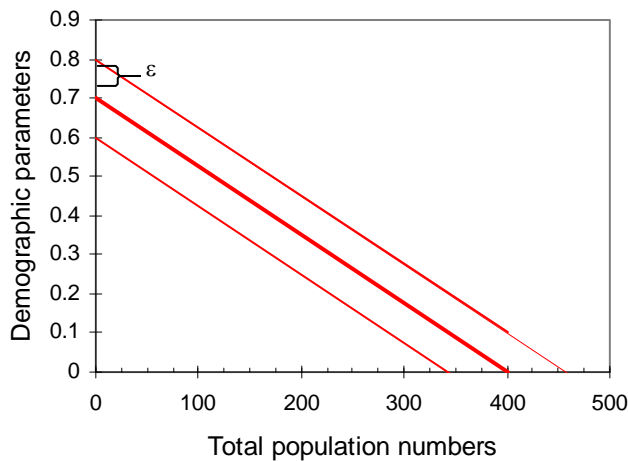
Density-dependence was introduced as a linear function of the total population numbers (Clutton-Brock & Lonergan, 1994). So, each of the four coefficients (survival and fecundity) described above are composed of two parameters, one for the intercept and one for the slope

(density-dependence). The function is decreasing and equals zero when the population



reaches its carrying capacity (Fig. 4).

Environment stochasticity was introduced as a stochastic coefficient affecting the intercept of the density-dependence function, the slope remaining unchanged. It implies that stochastic effect has the same influence on parameter, independent of density



(Fig. 4).

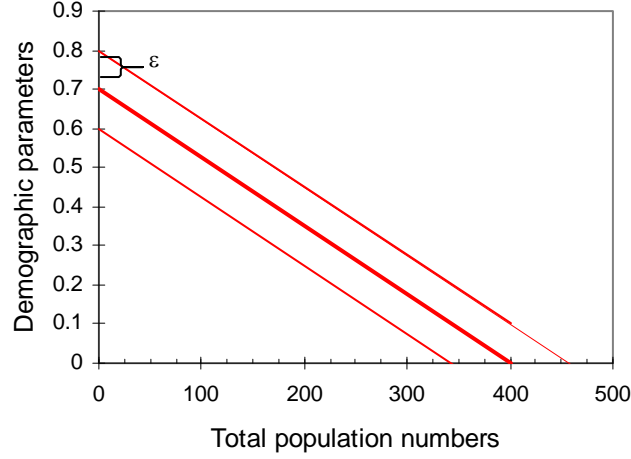


Fig. 4 : Linear density-dependence of the demographic parameters (fecundity and survival rates). The thick line is the fundamental function and the two thin lines define the range of the stochastic coefficient. Here, we have an intrinsic value of 0.7 and a carrying capacity of 400 individuals.

We have so the following recurrence equations :

General equation for all ages > 1 :

$$X_{a,s,t} = S_{a-1,s} X_{a,s,t-1} \quad (\text{Eq. 1})$$

Equation for age 1 :

$$X_{1,s,t} = \sum_{a=3}^{20} \frac{1}{2} F X_{a,f,t-1} \quad (\text{Eq. 2})$$

where

$X_{a,s,t}$ is the numbers of ibexes of age a , sex s at time t .

$X_{a,f,t}$ is the numbers of females of age a , at time t .

$S_{a,s}$ is the survival rate from age a to age $a+1$ of the sex s . (as explained above, $S_{a,s}$ can take only three values : S_y , S_a and S_o)

F is the fecundity of the females of age ≥ 3 .

a and t are integer numbers and measured in years.

The $\frac{1}{2}$ coefficient in Eq. 2 models the 1:1 birth sex ratio.

S and F are density-dependent and so obey to the following equations :

$$F = \alpha_F + \beta_F N_t \pm \varepsilon \quad (\text{Eq. 3})$$

$$S_y = \alpha_y + \beta_y N_t \pm \varepsilon \quad (\text{Eq. 4})$$

$$S_a = \alpha_a + \beta_a N_t \pm \varepsilon \quad (\text{Eq. 5})$$

$$S_o = \alpha_o + \beta_o N_t \pm \varepsilon \quad (\text{Eq. 6})$$

Where the intercepts α are the intrinsic values of their coefficient ; the slopes β are the negative effects of the population density ; ε is the stochastic coefficient which simulates the effect of climate, diseases, etc. ; N_t is the total population numbers at time t .

The model is thus driven by eight parameters, the two density-dependence parameters (α and β) defining density-dependent fecundity and survival rates.

Data and density-dependent parameters estimations

Census data are available for each Swiss Ibex colony since 1991. These data distinguish six sex and age classes : kids (< 1 year old), young individuals (1 to 2 years), adult females (age cannot be determined by field observation), males from 3 to 5 years, from 6 to 10 years, 11 years and older ; these classes have been chosen because they are easily distinguished on the field. For each of these classes, the numbers are known with high reliability. Furthermore, when culling was organised, we know the number and the class of the culled individuals. For some populations, we have longer series of data, sometimes since the reintroduction of the ibex in the region. The census are made early spring or early summer² and the cull in September.

On the basis of these data, we can estimate these parameters for each colony using the following process :

1° *Carrying capacity K*

The colony is assumed to follow a logistic dynamic :

$$\frac{1}{N} \frac{\Delta N}{\Delta t} = r \left(1 - \frac{N}{K}\right) \quad (\text{Eq. 7})$$

where :

N = total population numbers, r = intrinsic rate of increase, K = carrying capacity.

From biological data, the intrinsic increase r is fixed at an estimated maximal value of $r_{max} = 0.3$.

Furthermore, because of culling, we used relative production instead of relative increase :

$$\frac{\Delta N}{N}(t+1) = \frac{(N_{t+1} - N_t + C_t)}{N_t} \quad (\text{Eq. 8})^3$$

where C_t = numbers of culled ibexes in year t

So K could be estimated as the intercept with x axis of the line joining r_{max} and the « gravity centre » of census empirical data (Fig. 5), calculated as the average of $\Delta N/N$ and N .

² The June censuses seem to be less reliable than the April one, but we shall neglect it in this model.

³ If the census of one year or more is missing, we calculate the increasing rate between the two nearest years using the eq.9 divided by the number of years between them.

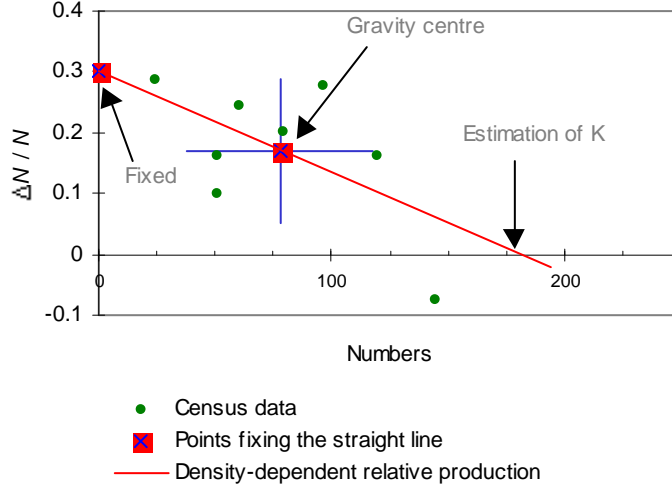


Fig. 5 : Method used to estimate the carrying capacity of the colony : we fix the first point at an estimated maximal value and we calculate the second as the gravity centre of the census data. See the text for additional explanations.

2° Calculation of the density-dependent parameters

We use the definition of the reproductive rate (R_0) which depends on the females Leslie's matrix (fecundity and survival rates). The general relation is :

$$R_0 = \sum_{a=1}^{20} \left(\prod_{i=1}^a S_i \right) F_a \quad (\text{Eq. 9})$$

(the product in brackets is the probability to be alive at the age a , sometimes noted l_a .)

Which in our case gives :

$$R_0 = \sum_{i=1}^{13} S_y^2 S_a^i F + \sum_{i=1}^4 S_y^2 S_a^{13} S_o^i F$$

In this last equation can we replace S_y , S_a , S_o and F by their density-dependent relation (Eq.3, 4, 5, 6) (with $\varepsilon = 0$) to obtain a density-dependent relation $R_0(N)$:

$$R_0 = \sum_{i=1}^{13} \left[(\alpha_y + \beta_y N)^2 (\alpha_a + \beta_a N)^i (\alpha_F + \beta_F N) \right] + \sum_{i=1}^4 \left[(\alpha_y + \beta_y N)^2 (\alpha_a + \beta_a N)^{13} (\alpha_o + \beta_o N)^i (\alpha_F + \beta_F N) \right] \quad (\text{Eq. 10})$$

Assuming a logistic dynamic we now attempt to express R_0 as a function of r , K and N :

For $N=0$: $\ln R_0 = rT$.

Stability implies that $R_0(N=K) = 2$ (so, $\ln R_0 = \ln 2$); effectively, when $N=K$, the numbers are stable and so each female must give birth in mean to two kids (one male and one female).

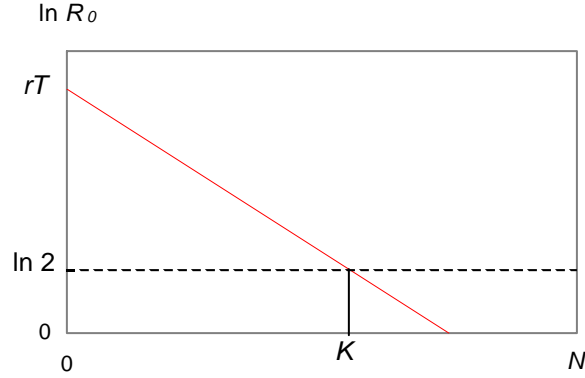


Fig. 6 : Reproductive rate R_0 in function of the density N . Assuming it follows a logistic dynamic, we know the points $(0 ; rT)$ and $(K ; \ln 2)$ and so we can calculate the equation of this function (see the text).

Furthermore, the logistic dynamic implies that $\ln R_0(N)$ is a linear function. As we know two points of the function we can calculate its equation (see Fig. 6) :

$$\ln R_0(N) = rT - N \frac{rT - \ln 2}{K}$$

i.e.

$$\boxed{R_0(N) = \exp\left\{rT\left(1 - \frac{N}{K}\right)\right\} 2^{\frac{N}{K}}} \quad (\text{Eq. 11})$$

Eq.11 gives us the theoretical function $R_0(N)$. We use it to calculate eight arbitrarily chosen points which permit us to evaluate numerically the eight parameters of the eq.11 by non linear regression. These eight parameters are so the ones resulting in the same logistic curve as defined by r and K .

Results and discussion

We present here some results for only one colony located in the Brienzer Rothorn in canton of Berne. It is followed since 1948, date of its foundation. It is culled since 1992.

The estimated carrying capacity is $K = 108$ individuals (Fig. 7). By bootstrapping, we obtain a mean value of 108.8 and 95% of the estimations are comprised between 86 and 136 (sample size = 500)

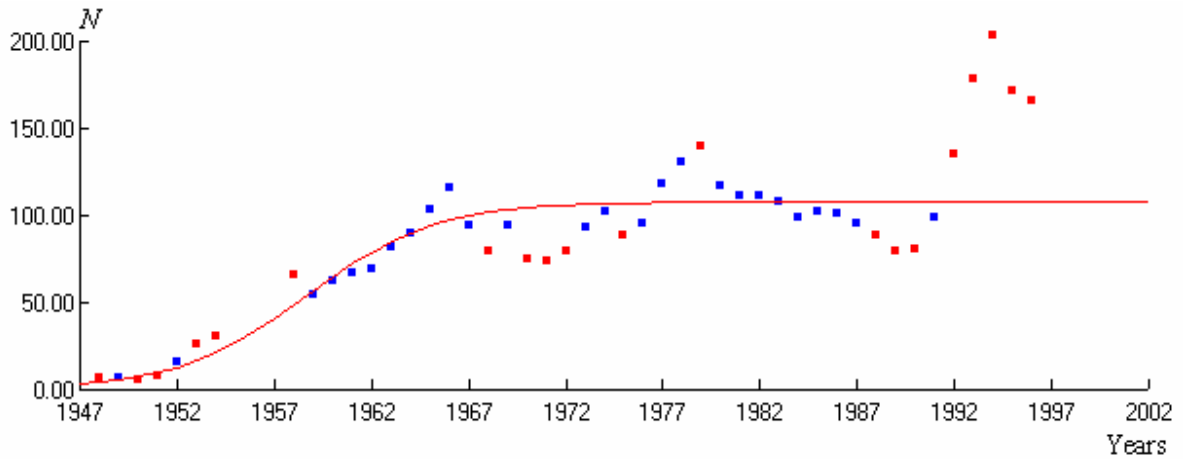


Fig. 7 : Evolution of the total numbers for the Brienzer Rothorn colony since its creation in 1948. The dots indicate the real data ; the line represents the logistic curve with $r = 0.3$ and $K = 108$ (Explained variance = 0.93)

The demographic parameters have been calculated for the five last years for which we dispose of age-structured data. The mean values are given in Tab. 1.

Tab. 1 : Demographic parameters for the Brienzer Rothorn colony. These values are the averages for the last five years. The adult survival greater than 1 could indicate immigration.

Colony	Mean value
Fecundity (F)	0.3
Youngs survival (S_y)	0.6
Adults survival (S_a)	1.1
Old survival (S_o)	0.5

As Fig. 7 shows it, the colony has reached its carrying capacity near 1964 and is since then oscillating around this value. Our estimation of $K = 108$ fit well to these data. According to this value, the colony largely exceeded its carrying capacity since five years ago. This corroborates the field observations which have conducted fauna managers to introduce culling since 1992.

The mean value of the fecundity seems too low accordingly to fauna managers preconceptions (females are thought to give birth once in two years). Young and old survival rates fit well to the known demography.

Adult survival exceeds 1 and is so evidently too high. This could be explained by immigration from adjoining colonies. If we pool the data of this populations with that of the neighbouring Augstmatthorn colony, adult survival rate become lower than 1.

This observation suggests that the assumption of closed systems is not totally true . Field observations give similar indications ; in winter particularly, ibexes can travel through vast area and are so susceptible to pass in an adjacent colony. We intend now to improve the fit of our model to field data and include the effect of migrations on populations dynamic.

This model is used to test different culling strategies through stochastic simulations. The choice criterions are : 1° minimise extinction risk ; 2° minimise impact on environment ; 3° equilibrate the age and sex structure (ORB, 1991).

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