

DENSITY DEPENDENCE EFFECTS IN A CHAMOIS POPULATION  
OF THE ITALIAN ALPS

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**ABSTRACT**

This paper's goal is to determine the relative importance of exogenous (snowcover) and endogenous factors (density dependence) in the dynamics of a chamois population of the Italian Alps, for which a reasonably long record of detailed data is available. While probing the two types of factors, we take into account that density might affect the demographic parameters with a time delay.

## INTRODUCTION

Two basic forces govern the dynamics of a population (Royama, 1977; Berryman, 1981, 1991; Berryman et al, 1987): exogenous driving or disturbance (density independent factors) and endogenous density induced feedback (density dependent factors). Despite the long pending controversy between Nicholson's view and Andrewartha and Birch's, it is now widely accepted that, depending on circumstances, one or the other or both of these forces may be the actual determinants of the observed time course of populations numbers or biomasses.

Density independent factors have been traditionally considered more important for mountain than for other ungulates (Kuck, 1977; Schröder, 1985); nevertheless, several authors suggested density dependence as an important determinant of the population dynamics of one of the most abundant European mountain ungulates, the chamois (*Rupicapra rupicapra*) (Peracino and Bassano, 1987; Tosi and Perco 1981; Schröder 1971, 1985). Schröder (1971) proposed the logistic model as a good descriptor of the dynamics of chamois in Austria, but, although intraspecific competition for food was suggested as a mechanism for density dependence, he did not present any statistical or experimental evidence for that. On the other hand, Schröder himself (1971) found a correlation between young mortality and snowcover. As Schröder (1985) proposed young mortality in winter as an important determinant of chamois abundance, this seems to imply that an exogenous factor (weather) is actually driving the numbers of chamois populations. Other studies (Balbo et al., 1985, and Peracino and Bassano, 1987), however, suggest a close relationship between density dependent mortality and parasitic and infectious disease for chamois populations in France and Italy. To complete the picture, predation by fox and eagle (which through the predators' functional and numerical response is density dependent) acts on juvenile chamois as a source of mortality. In fact, it is known that chamois is an important component in the diet of the king eagle (*Aquila chrysaëtus*) (Praz

and Felay, 1974, Clout, 1981; Henninger et al, 1986) and eagle attacks on chamois kids were observed (Couturier, 1938; Krämer, 1969); however, there is no agreement about how important eagle predation is for chamois. While Schröder (1971) and Peracino and Bassano (1987) suggested that eagle predation produces minimal effects on population dynamics, Ferrario (1980) proposed eagle predation as relevant for kid survival.

This paper's goal is to determine the relative importance of exogenous (snowcover) and endogenous factors in the dynamics of a chamois population of the Italian Alps, for which a reasonably long record of detailed data is available. While probing the two types of factors, we take into account that density might affect the demographic parameters with a time delay. The importance of this point was already noticed by Volterra (1934) long time ago and reiterated by May (1973) and May et al (1974). Despite that, only recently time lags have been explicitly incorporated in the analysis of population time series. With reference to insects, Turchin (1990) showed that populations that were considered density independent actually presented delayed density effects, while Royama (1992) found evidence of lagged density dependence in the natality of snowshoe hare. Delayed density dependence is expected to arise as a result of interspecific interactions (predation, competition, parasitism, ...) and/or population structure (Royama, 1977, 1981; Murdoch and Reeve 1987, Turchin, 1990, Turchin and Taylor, 1992; Berryman, 1991), which is certainly the case for chamois.

## **MATERIALS AND METHODS**

### ***Field data***

Data were collected in *Azienda Faunistica di Barbellino -Valbelviso* , a preserve where controlled hunting is permitted. The area is located in Lombardy (Provincia di Sondrio), Italy and is a typical Alpine habitat with rocky areas and steep slopes, surrounded by forests with a rich underbrush. Hunting, eagle predation, parasitism and epidemic diseases

act on the chamois population as sources of mortality. In fact, hunting takes about 8% of the population each year, while a pair of king eagle (*Aquila chrysaëtus*) has been present in this area for more than 10 years (Tosi 1989) and their diet, which is well known (Ferrario, 1980), includes chamois kids. Also, epidemic diseases, such as keratonconjunctivitis, and intestinal infections from parasitic nematodes are a major cause of mortality (Genchi et al. 1983, Tosi 1989).

The chamois living in this area can be considered a closed population. It has been observed that chamois from the neighboring area (*Val di Scalve*) incidentally come into contact with animals of our study area in summer, after reproduction, when higher temperature permits walking to the upper portion of the valley.

The bulk of data consists of total censuses of animals divided by sex and age category (kid, yearling, 2-3-years-old adult and 4-years-old and older adult) from 1981 to 1990 (Fig 1a-c). They were collected by direct observation from strategic points. The whole area was divided in different territory units isolated one from another in order to avoid interarea displacement. For example, a valley surrounded by improductive areas is a unit. Each unit was divided in small parcels which were distinguished either by clear boundary lines (little valleys, hills) or by differences in vegetation cover and structure. Each parcel was assigned to an observer who was located in the most suitable point of observation. The census was performed every year in June-July, before the hunting season and after reproduction in order to evaluate winter mortality and birth rate. The counts were made during the 4 hours following sunrise because this is the period of greatest activity (Tosi and Scherini 1989, Pedrotti 1990). This census methodology is similar to the block count method (Maruyama and Nakama, 1983) and to the flash pointing census (Berdecou and Bouses, 1985). Animals' sex and age were recognized by behavioral, anatomic and morphological characteristics, according to the classification of Meile and Bubenick (1979). It is not possible to recognize the sex of kids from afar, but the assumption of a 1:1 sex ratio is very reasonable (Caugley, 1970). The sex of a few yearlings and adults could not be recognized;

therefore, we allocated these undetermined animals to the two sexes, using the same ratio found in the animals for which sex could be clearly established.

In addition to data from censuses, information on the number of animals hunted and on the number of carcasses found in the field is also available from 1981 to 1990. In both cases data are classified by age and sex (Table 2 and 3).

### *Calculation of population parameters*

Chamois populations are characterized by a short reproductive season during the spring and are therefore best described by discrete-time demographic models. Also, hunting is allowed only during a short period in late summer. Due to these facts, we have chosen to work with population parameters calculated as finite rates.

The rate of increase ( $R_t$ ) of the population is calculated as  $N_{t+1}/N_t$ , where  $N_t$  is the total number of individuals in year  $t$ . The finite birth rate is obtained as the number of female kids (half the total number of censused kids) in year  $t$ , divided by the number of reproductive females in year  $t$ . We consider two-year-old and older females as potential mothers (Caughley, 1970; Valentencic et al, 1974; Bauer, 1985). The finite natural death rate is computed as the number of animals that die from natural causes between year  $t-1$  and  $t$ , divided by the number of animals censused in year  $t-1$ . We separately calculate a total death rate, a death rate for yearling plus adult females, one for yearling plus adult males, and one for kids. The relevant number of died animals is calculated in two different ways: (1) by using the carcasses found in the field between year  $t-1$  and year  $t$ , though this only allows calculation of an index of the natural death rate, (2) by calculating the difference between subsequent annual censuses in the following way:

#### Total natural death rate

The global balance between births and deaths is as follows

$$M_{t-1} = N_{t-1} - N_t + K_t - H_{t-1} \quad (1)$$

where

$M_{t-1}$  is the total number of animals that die from natural causes between year  $t-1$  and year  $t$ ,

$N_t$  is the total number of animals in year  $t$ ,

$K_t$  is the number of kids in year  $t$ ,

$H_{t-1}$  is the number of animals shot in year  $t-1$ .

The finite death rate is given by  $M_{t-1}/N_{t-1}$

#### Natural death rate of yearlings and adults

Within this population segment the balance is given by

$$MA_{t-1} = A_{t-1} - A_t + Y_{t-1} - HA_{t-1} \quad (2)$$

where

$MA_{t-1}$  is the number of one-year-old or older males or females that die naturally between year  $t-1$  and year  $t$ ,

$A_t$  is the number of male or female adults (two-years-old or older individuals) in year  $t$ ,

$Y_{t-1}$  is the number of male or female yearlings in year  $t-1$ ,

$HA_{t-1}$  is the number of one-year-old or older male or female chamois harvested in year  $t-1$ .

The finite death rate within this age group is provided by  $MA_{t-1}/(A_{t-1} + Y_{t-1})$

#### Natural death rate of kids

The balance of kids is as follows

$$MK_{t-1} = K_{t-1} - TY_t - HK_{t-1} \quad (3)$$

where

$MK_{t-1}$  is the number of kids that die naturally between year  $t-1$  and year  $t$ ,

$TY_t$  is the total number of yearlings in year  $t$ ,

$HK_{t-1}$  is the number of kids harvested in year  $t-1$ .

The finite death rate is given by  $MK_{t-1}/K_{t-1}$ .

The above computations for the natural death rates assume there is no compensatory effect between natural and hunting-related deaths. If this is true, then the total death rate is provided by the sum of the natural finite death rate and the hunting-related death rate. On the other hand, if compensation were acting, we would expect a negative correlation between natural and hunting-related death rates. To test for this hypothesis, we have used the index of natural mortality (calculated from carcasses) as an independent estimator of the natural finite death rate. Moreover, as the total and natural mortality might present density dependence, as anticipated in the Introduction, we have actually calculated the correlation between the ratio of the index of natural mortality to the total finite death rate and the ratio of hunting-related death rate to the total finite death rate. This latter has been obtained from Eq. 1 as:

$$D_{t-1} = 1 + B_{t-1} - R_{t-1} \quad (4)$$

where

$D_{t-1}$  is the total finite mortality rate between year  $t-1$  and year  $t$ ,

$B_{t-1}$  is a crude finite birth rate, calculated as the kid number in year  $t$  divided by the total number of animals in year  $t-1$ ,

$R_{t-1}$  is the finite rate of increase, calculated as  $N_t$  divided by  $N_{t-1}$ .

Pearson, Kendall and Spearman correlation coefficients between the two ratios have been estimated. We expect that at least one of them is negative and significant if there exists compensation between natural and hunting-related deaths.

### ***Dependence of demographic parameters upon exogenous factors***

Schröder (1973) found that winter mortality is correlated with snow height. Also, Schröder (1985) suggested that the average amount of snow drives the population size of chamois.

To determine the effect of weather on population parameters we perform regressions of the finite rate of increase, the finite birth rate, the finite death rate (total, one-year-old and older males, one-year-old and older females and kids) and the absolute number of died animals (total, one-year-old and older males, one-year-old and older females and kids) against three statistics of the snow height in winter: the maximum, the average and the standard deviation. Snow data come from a measurement station located in the study area (Stazione di Serbatoio, Diga di Frera) and were kindly provided by the River Adda Authority (Consorzio dell' Adda).

***The effect of density on the rate of increase, the birth rate and the death rate***

The best way to study density dependence is by doing experiments. These usually consist of artificially reducing or increasing the population size and observing: (a) if the population returns to the original level or pattern of temporal variation, (b) whether there is a corresponding variation in some demographic parameters (Murdoch, 1970, Massot et al. 1992 and references quoted therein). However, carrying out this kind of experiments with large mammals would pose formidable problems and therefore density manipulations are not usually performed.

It follows that the statistical analysis of series of sequential censuses is the commonest approach. Morris (1963) was possibly the first who proposed to make a regression between  $\ln N_t$  and  $\ln N_{t-1}$ . Density dependence can be inferred if the slope of the regression line is smaller than unity. Several authors strongly criticized this method because false density independence might result (Eberhardt, 1970; Maelzer, 1970; St. Amant, 1970; Luck, 1971; Kuno, 1971; Itô, 1972; Benson, 1973; Pielou, 1974; Dempster, 1975). Varley and Gradwell (1963), Slade (1977) and Vickery and Nudds (1984) proposed different tests of regression to estimate density dependence. However, Gaston and Lawton (1987) and Pollard et al. (1987) showed that all of them rejected density dependence when

it was detected by other ways. In fact, all of the above models are appropriate for describing and analyzing density-dependent population dynamics when there are no time lags in the feedback response. Bulmer (1975) was the first to propose an autoregressive time series model of  $\ln N_t$  and the use of autocorrelation functions, but he restricted his attention to nondelayed effects. Turchin (1990) extended the concept to the case when delays are present and suggested the use of partial autocorrelation functions to estimate how delayed the feedback response is. Nevertheless, these nonparametric methods seem to be powerful only when long runs of data are available (Solow, 1990; Solow and Steele, 1990). For this reason, more recently Berryman and Millstein (1990), Turchin and Taylor (1992) and Berryman (1992) suggested to resort to a more sparing, parametric approach by simply performing linear and nonlinear regressions between  $\ln R_{t-1}$  and the lagged densities  $N_{t-T}$  ( $T \geq 1$ ). The lengths of the time lags should be those that produce the maximum significant coefficient of determination ( $r^2$ ). We basically follow this approach and perform linear regressions of  $\ln R_{t-1}$  against the lagged densities  $N_{t-T}$ . We then search for the most significant regression. If none is significant, we proceed to perform nonlinear regressions. Prior to this statistical analysis, we also perform an approximate analysis based on a graphical approach (Royama, 1977; Berryman and Millstein, 1990). It consists of plotting  $\ln R_{t-1}$  against  $N_{t-T}$  for different time delays  $T$ . If the trajectory obtained by joining points corresponding to successive years presents a clockwise trend,  $t$  is an underestimate of the actual delay; on the contrary  $T$  is an overestimate if the trajectory has a counterclockwise trend. The estimate is approximately correct when no such trend is detectable.

To estimate the effect of density on the birth rate and the different death rates, we note (see Eq. 4) that

$$\ln R = \ln(1+B-D) \approx B-D$$

and therefore it seems logic to perform linear and (if necessary) nonlinear regressions of the finite rates against  $N_{t-T}$ . Density dependence is then ascertained on the basis of the coefficient of determination.

## RESULTS

### *Compensation between natural and hunting-related deaths*

The correlation between the ratio of natural to total death rate and the ratio of hunting-related to total death rate results nonsignificant at the 95% confidence level ( $r(\text{Pearson})=0.15$ ,  $P=0.69$ ;  $t(\text{Kendall})=0.22$ ,  $P=0.40$ ;  $r(\text{Spearman})=0.33$ ,  $P=0.34$ ). This suggests that there is no compensation between natural and hunting mortality. Therefore, we conclude that it is possible to calculate natural mortality in the various segments of the chamois population as suggested in the previous section.

### *The effect of snow cover on the rate of increase, the birth and death rates*

The simple regressions between growth rate and the maximum height of snow in the winter, the average height of snow in the winter and the standard deviation of the average height of snow in the winter result non statistically significant ( $P=0.49$ ,  $P=0.30$ ,  $P=0.43$ , respectively).

Also the simple regression between birth rate and the maximum height of snow in the winter, the average height of snow in the winter and the standard deviation of the average height of snow in the winter result non statistically significant ( $P=0.32$ ,  $P=0.21$ ,  $P=0.44$ , respectively).

Similar results present the simple regressions between death rate and the maximum height of snow in the winter, the average height of snow in the winter and the standard deviation of the average height of snow in the winter, with  $P=0.67$ ,  $P=0.48$ ,  $P=0.66$ , respectively; the simple regressions between one year old and older males death rate and the maximum

height of snow in the winter, the average height of snow in the winter and the standart deviation of the average height of snow in the winter, with  $P= 0.44$ ,  $P= 0.19$ ,  $P= 0.42$ , respectively; the simple regressions between one year and older females death rate and the maximun height of snow in the winter, the average height of snow in the winter and the standart deviation of the average height of snow in the winter, with  $P= 0.30$ ,  $P= 0.15$ ,  $P= 0.20$ , respectively; and the simple regressions between kids death rate and the maximun height of snow in the winter, the average height of snow in the winter and the standart deviation of the average height of snow in the winter, with  $P= 0.46$ ,  $P= 0.32$ ,  $P= 0.52$ , respectively.

Also the simple regressions between total number of death animals and the maximun height of snow in the winter, the average height of snow in the winter and the standart deviation of the average height of snow in the winter ( $P= 0.80$ ,  $P= 0.90$ ,  $P= 0.89$ , respectively); the regressions between the number of one year old and older died males and the maximun height of snow in the winter, the average height of snow in the winter and the standart deviation of the average height of snow in the winter ( $P= 0.72$ ,  $P= 0.40$ ,  $P= 0.68$ , respectively); the regressions between the number of one year and older died females and the maximun height of snow in the winter, the average height of snow in the winter and the standart deviation of the average height of snow in the winter ( $P= 0.52$ ,  $P= 0.32$ ,  $P= 0.36$ , respectively); and the regressions between the number of died kids and the maximun height of snow in the winter, the average height of snow in the winter and the standart deviation of the average height of snow in the winter ( $P= 0.39$ ,  $P= 0.41$ ,  $P= 0.54$ , respectively), are non satistically significant.

***Density dependence in the rate of increase, the birth and the death rates***

The regression between  $\ln R$  and  $N_{t-T}$  is not significant for  $T$  equal to 1 ( $P= 0.14$ ), but it is significant for  $T$  equal to 2 ( $P= 0.025$ ) and for  $t$  equal to 3 ( $P= 0.007$ ). The coefficient of determination  $r^2$  is bigger for  $T = 3$  ( $r^2=0.78$ ) than for  $T = 2$  ( $r^2=0.59$ ). On the other hand,

the trajectory produced by plotting  $\ln R_{t-1}$  vs.  $N_{t-T}$  is circular and clockwise for  $T = 1$  (Fig. 2a), straight and clockwise for  $T = 2$  (Fig. 2b), but it is straight and counterclockwise for  $T = 3$  (Fig. 2c). These results suggest a density-dependence effect on the instantaneous rate of population increase with a delay of 3 years; however, 2 years' delay cannot be rejected. In the Fig. 2d we could see the fitted regression model for  $T = 3$ .

All linear regressions between birth rate and  $N_{t-T}$  result nonsignificant at the 5% confidence level (for  $T = 1$ ,  $P = 0.91$ ;  $T = 2$ ,  $P = 0.26$ ;  $T = 3$ ,  $P = 0.07$ ) (Fig. 3a-c). The Fig. 3d shows the fitted linear regression (with interception equal to zero) between the number of females kids against the number of adult females which results highly significant ( $P < 0.0001$ ,  $r^2 = 0.99$ ). These results suggest independence between finite birth rate and density.

Considering the effect of density on mortality, we first analyze the indices of finite death rate obtained from carcasses. It turns out that the index for the total number of individuals, that for one-year-old and older males, that for one-year-old and older females and that for kids all present nonsignificant linear regression against  $N_{t-1}$  ( $P = 0.24$ ;  $P = 0.12$ ;  $P = 0.15$ ;  $P = 0.12$  respectively). We obtain similar results when we do the regressions against  $N_{t-2}$  ( $P = 0.31$ ;  $P = 0.18$ ;  $P = 0.13$ ;  $P = 0.86$ ). The regressions against  $N_{t-3}$  (Fig. 4a-d) result significant for the total number of chamois ( $P = 0.006$ ,  $r^2 = 0.804$ ), for one-year-old and older males ( $P = 0.0004$ ,  $r^2 = 0.935$ ) and one-year-old and older females ( $P = 0.00001$ ,  $r^2 = 0.987$ ), while that for kids is not significant ( $P = 0.28$ ). These results suggest that death rate is density dependent with 3 years' delay, although this is not true for kids. To complement the linear regression analysis, we perform exponential regressions, which have the biological advantage of predicting a nonnegative death rate over the whole range of densities. It turns out (Fig. 4) that for  $T = 3$  we have the same three significant cases as in the linear regression, although the confidence level is lower in two out of three ( $P = 0.0015$ ,

$r^2= 0.887$  for the total number of individuals;  $P= 0.004$ ,  $r^2= 0.838$  for one-year-old and older males,  $P=0.04$ ,  $r^2= 0.832$  for one-year-old and older females).

As for the finite death rates computed from censuses, we have that the finite death rate for the total number of individuals, for one-year-old and older males, for one year old and older females and for kids present nonsignificant linear regressions against  $N_{t-1}$  ( $P=0.08$ ;  $P=0.13$ ;  $P=0.29$ ;  $P=0.42$  respectively). When we do the linear regressions against  $N_{t-2}$ , significant results are obtained for the total death rate ( $P= 0.03$ ) and the mortality of one-year-old and older males ( $P= 0.05$ ), nonsignificant for one-year-old and older females ( $P=0.38$ ) and for kids ( $P=0.24$ ). The linear regressions against  $N_{t-3}$  (Fig. 5) result significant for the total number of individuals ( $P=0.01$ ,  $r^2= 0.747$ ), for one-year-old and older males ( $P=0.02$ ,  $r^2= 0.702$ ), for one-year-old and older females ( $P= 0.005$ ,  $r^2= 0.821$ ) and for kids ( $P=0.045$ ,  $r^2= 0.585$ ). These results suggest that death rate is density dependent with a delay of 3 years for all the population segments, kids included. Similarly to the previous case (index of death rate from carcasses), we complement the linear regression by performing exponential regressions for  $T =3$ . These are somehow less significant than the linear ones ( $P=0.047$ ,  $r^2= 0.579$  for total number of individuals;  $P= 0.048$ ,  $r^2= 0.576$  for one-year-old and older males;  $P=0.003$ ,  $r^2= 0.846$  for one-year-old and older females,  $P= 0.045$ ,  $r^2=0.584$  for kids). However, they have advantage of a greater biological meaning, because rates are nonnegative over the whole range of densities.

The problem of mortality in kids deserves further attention. In fact, the results obtained by using the two different indices of mortality (from carcasses and from subsequent censuses) are not conclusive about density dependence. While the consecutive census analysis suggests density dependence with 3 years' delay, the analysis of carcasses suggests that density plays no role in the mortality of kids. This discrepancy might be due to the effect of predation, mainly performed by the red fox and the eagle. The first one is a scavenger, which hides or destroys the kid carcasses, while the second captures kids and carries them

to its nest. In both cases, the kid carcasses are not recoverable on the ground and this may considerably alter the index of kid death rate as calculated from carcasses.

The importance of predation, as a mortality source for kids only, suggests that kid death rate might basically depend upon the density of kids, not the total density. In fact, we expect that predators respond, numerically or functionally, to the specific density of the age class they can prey upon. This can explain why the kid death rate, calculated from censuses, shows a poor correlation with total density. For this reason, we have decided to make a regression of the kid death rate not only against total density, but also against kid density. As apparent from Fig. 6, the relationship is nonlinear. We have tried with a model of the following form:

$$KD_{t-1} = a + b K_{t-1} + c K_{t-1}^2 + d N_{t-3}$$

where

$KD_{t-1}$  is the finite kid death rate between year t-1 and year t,

$a$ ,  $b$ ,  $c$  and  $d$  are parameters of the model.

The fit between the model and the data (Fig. 6) is quite good ( $P < 0.001$ , adjusted  $r^2=0.916$ ) and shows that the part of variance in the death rate that is not explained by the delayed total density can be explained by kid density. Since there exists inverse density dependence at low kid density, the model is characterized by depensation. As a matter of fact, an Allee effect might result from the concurrence of a weak numerical response of predators and a saturation in their functional response (Begon et al., 1990, pp. 353-55). For instance, Ferrario (1980) observed that a pair of eagle living in the area of study consumed 10 kids in each reproductive season, irrespective of kid density

## DISCUSSION

The effect of snow resulted of few importance as a driven force of chamois population on *Azienda Faunistica di Barbellino Valbelviso*. This result is against the results found by Schröder (1971, 1985) for a population of chamois at Austria, in which the height of snow

resulted in a driven force of population abundance. The effects of density resulted a key to understand the dynamics of this population, although in mountain ungulates exogenous factors are consider more important for determining the population abundance (Schröder 1985, Kuck 1977). The population presented a delay on the effect of density in the growth rate equal to 3. The time lags greater than one in density dependence are related to the effect of trophic relationships like numerical response of predators, parasites or pathogens (Berryman 1981, Berryman et al 1987, Berryman and Millstein 1990). In the population on study, it was observed a big number of gastrointestinal parasites during the years of highest density (1981, 1982) (Genchi et al. 1983, Tosi 1989) but the lowest value of growth rate was during the keratoconjunctivitis epidemic in 1984 (Tosi 1989). It was consider that the risk to epidemic is higher when the population is over 20 individuals by  $\text{km}^2$  (Balbo et al 1985). The population reached this value in 1981, therefore the epidemic happened with a delay of 3 years. Our results are consistent with the Peracino and Basano (1985) suggestion about the keratoconjunctivitis are related with intraspecific competition.

Although the birth rate is not affected by the density, the analysis of the effect of density on mortality rate confirms the results on growth rate. Although delay of 2 years is significant in same cases (total number of individuals and one year old and older males using a death rate calculate by consecutive census), delays of 3 years are significant in all cases. The exponential regressions with a delay of 3 years although in some cases with less statistical signification than lineal regression, explain the density dependence with the most biological meaning. It is true because they do not required immigration.

For kids the regression between the index of death rate and  $N_{t-3}$  results non significant however the regression between the kid death rate and  $N_{t-3}$  results significant. The number of kid carcasses could be wrong because of the action of scavenger as red fox and predator as king eagle. The effect of the last one could explain the high  $r^2$  for the non linear regression between the kid death rate between  $t-1$  and  $t$ , and the kid number in  $t-1$  and  $N_{t-3}$ . This quadratic regression suggested Allee effect in kid death rate, when there is low level

kid abundance and direct effect when there is high abundance. The Allee effect could be a consequence of a couple of eagle present in the study area (Tosi 1989) which consumes 10 kids in a reproductive season (Ferrario 1980). Although the effect of eagle predation has been consider irrelevant for chamois population dynamics (Schröder 1971, Peracino y Basano 1987), our results suggested it is necessary to pay more attention to the effect of that predation. By other hand the direct effect of high kid abundance could be related with intraspecif competition. Capurro (1991) shows that the number of kids is proportional with the number of females, therefore an increase in kid abundance means an increase in female abundance. The increase in female number could produce intraspecif competition for grass. This competition could reduce the state of health of kids at born or the quality of milk produce by females. Tosi (1989) compared the weight of female between the year of 1981 (highest density) and the years 1984 and 1985 (lowest density). He observed a decrease in weight with high density. This effect would not be reflected in adult death or in the birth rate but would affect the mortality of kids.

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Figure 1. Census data for chamois population in the *Azienda Faunistica de Barbellino-Valbelviso* from 1981 to 1990. *a*- Total number of chamois individuals and total number of chamois' kids. *b*- Female number in the different ages categories (I= one year old, II= 2-3 years old, III= 4 -10 years old, IV= 11 and older ). *c*- Male number in the different ages categories.

Figure 2. Effect of lagged abundance of chamois ( $N_{t-T}$ ) on the instantaneous growth rate ( $\ln R_{t-1}$ ) for chamois population in the *Azienda Faunistica de - Barbellino-Valbelviso* from 1981 to 1990. *a*-Trajectory of  $\ln R_{t-1}$  against  $N_{t-1}$  . *b*-Trajectory of  $\ln R_{t-1}$  against  $N_{t-2}$  . *c*-Trajectory of  $\ln R_{t-1}$  against  $N_{t-3}$  . *d*- Linear regression model fitted between  $\ln R_{t-1}$  and  $N_{t-3}$  ( $P=0.07$ ,  $r^2=0.78$ ).

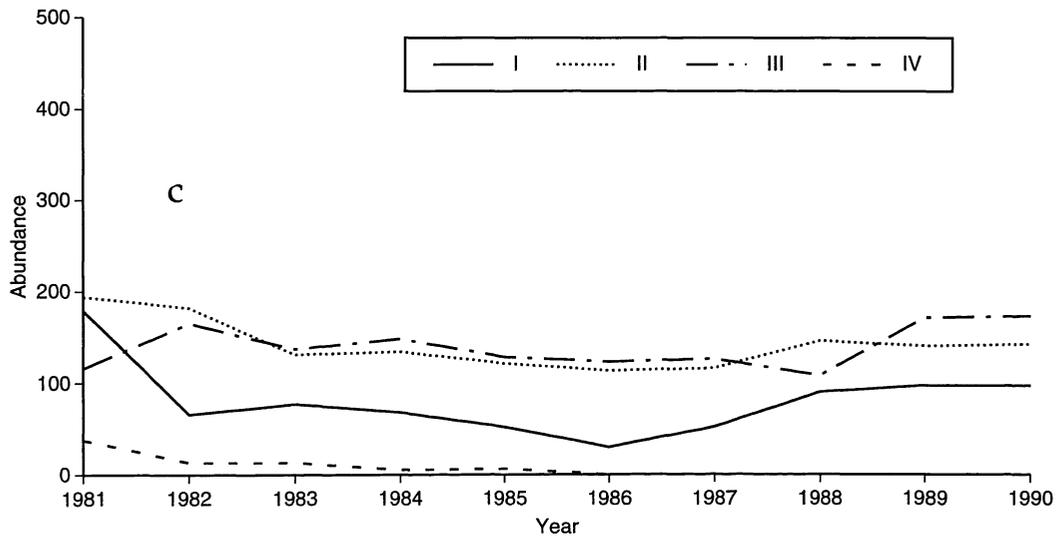
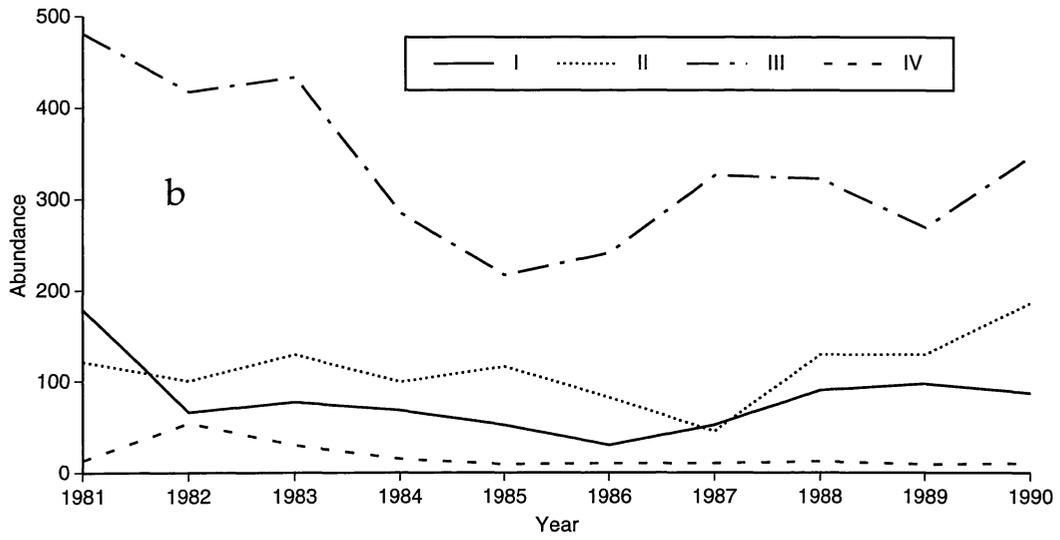
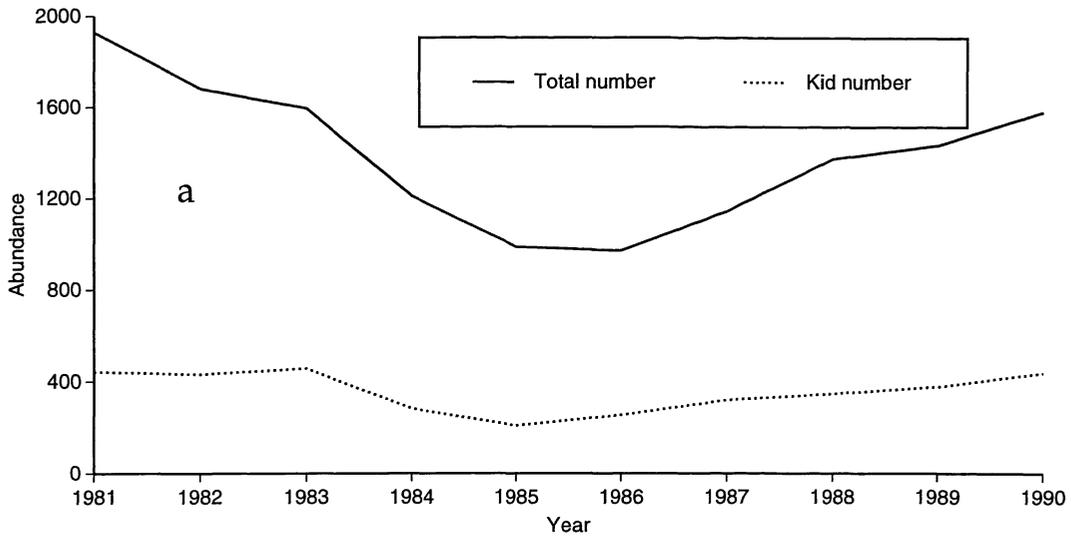
Figure 3. Effect of lagged abundance of chamois ( $N_{t-T}$ ) on the birth rate for chamois population in the *Azienda Faunistica de - Barbellino-Valbelviso* from 1981 to 1990. *a*- regression against  $N_{t-1}$  (non significant,  $P=0.91$ ). *b*- regression against  $N_{t-2}$  (non significant,  $P=0.26$ ). *c*- regression against  $N_{t-3}$  (non significant,  $P=0.07$ ). *d*- regression (Cero) between kids number and adult female number (highly significant,  $P < 0.0001$ ).

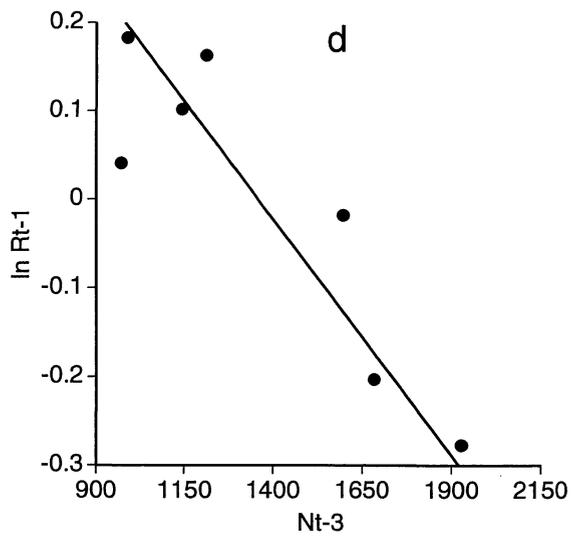
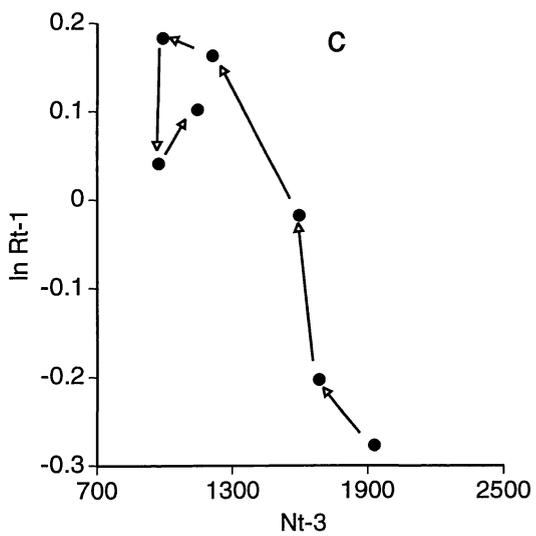
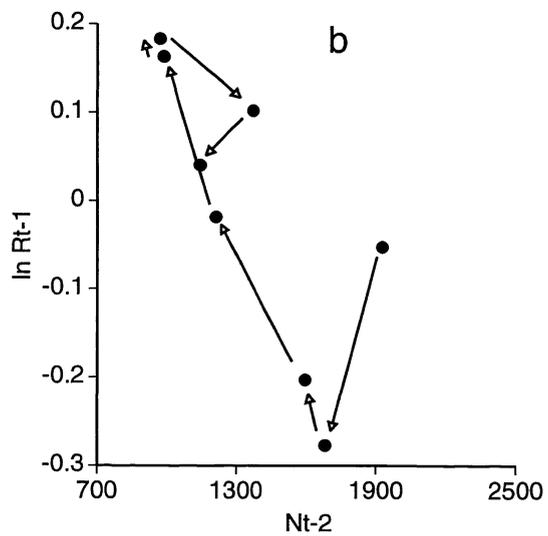
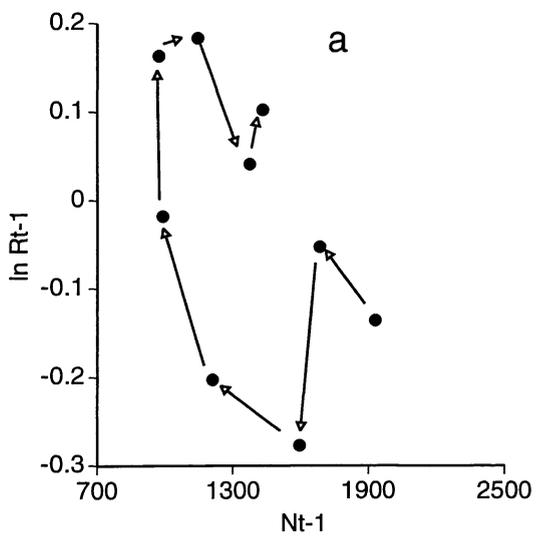
Figure 4. Linear and exponential regression between index of death rate from carcasses and three years lagged abundance of chamois ( $N_{t-3}$ ) for chamois population in the *Azienda Faunistica de - Barbellino-Valbelviso* from 1981 to 1990. *a.* Index for total number of chamois (idt) (linear  $P=0.006$ ,  $r^2=0.80$ , exponential  $P=0.0015$ ,  $r^2=0.88$ ). *b.* Index for number of male chamois of one year old or older (idm) (linear  $P=0.004$ ,  $r^2=0.93$ , exponential  $P=0.004$ ,  $r^2=0.83$ ). *c.* Index for total number of female chamois of one year old or older(idf) (linear  $P<0.001$ ,  $r^2=0.98$ , exponential  $P=0.004$ ,  $r^2=0.83$ ). *d.* Index for total number of kid chamois (idk) (linear  $P=0.28$ ,  $r^2=0.22$ , non significant, exponential  $P=0.48$ ,  $r^2=0.34$ , non significant)

Figure 5. Linear and exponential regression between finite death rate from carcasses and three years lagged abundance of chamois ( $N_{t-3}$ ) for chamois population in the *Azienda Faunistica de - Barbellino-Valbelviso* from 1981 to 1990. *a.* Rate for total number of chamois (fdt) (linear  $P=0.01$ ,  $r^2=0.74$ , exponential  $P=0.047$ ,  $r^2=0.57$ ). *b.* Rate for number of male chamois of one year old or older (fdm) (linear  $P=0.02$ ,  $r^2=0.70$ , exponential  $P=0.047$ ,  $r^2=0.58$ ). *c.* Rate for total number of female chamois of one year old or older(fdf) (linear  $P=0.005$ ,  $r^2=0.82$ , exponential  $P=0.048$ ,  $r^2=0.57$ ). *d.* Rate for total number of kid chamois (fdk) (linear  $P=0.04$ ,  $r^2=0.58$ , exponential  $P=0.045$ ,  $r^2=0.58$ )

Figure 6. Polynomial regression between kid death rate against kid density for chamois population in the *Azienda Faunistica de Barbellino-Valbelviso* from 1981 to 1990 ( $P<0.001$ , adjusted  $r^2=0.91$ ).

FIG 1





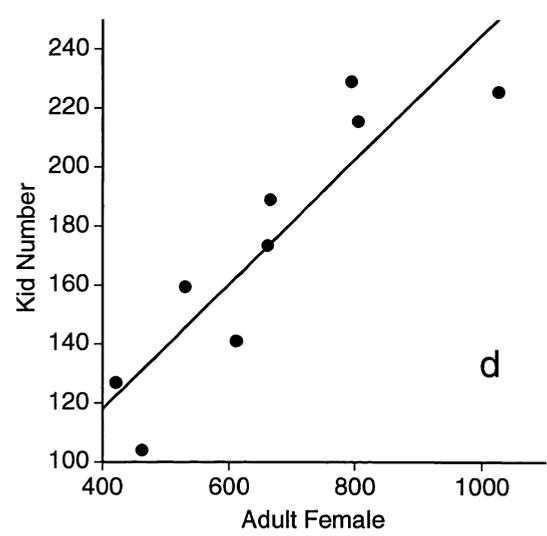
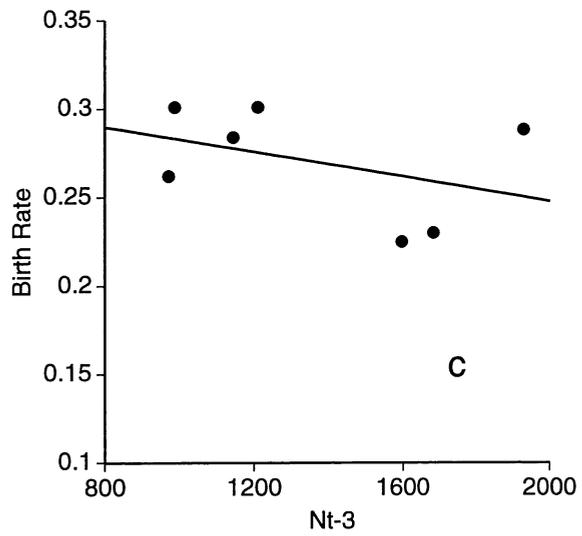
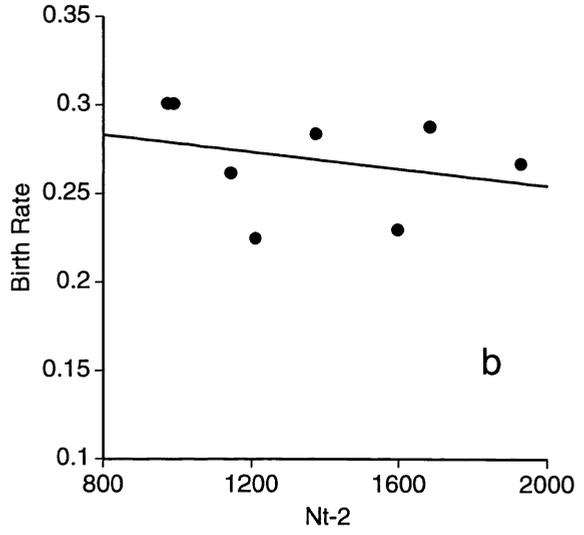
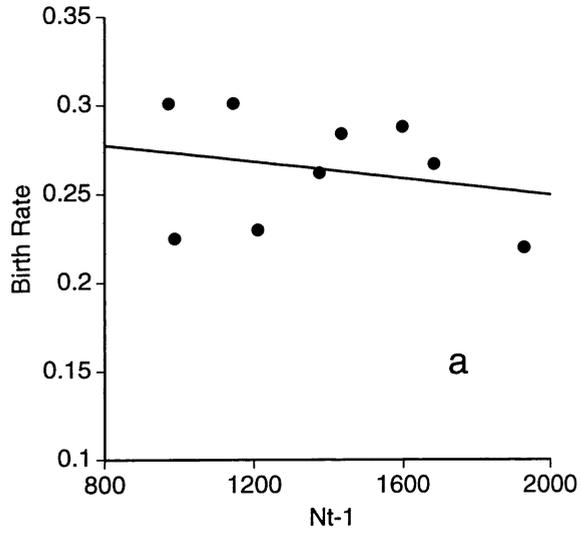
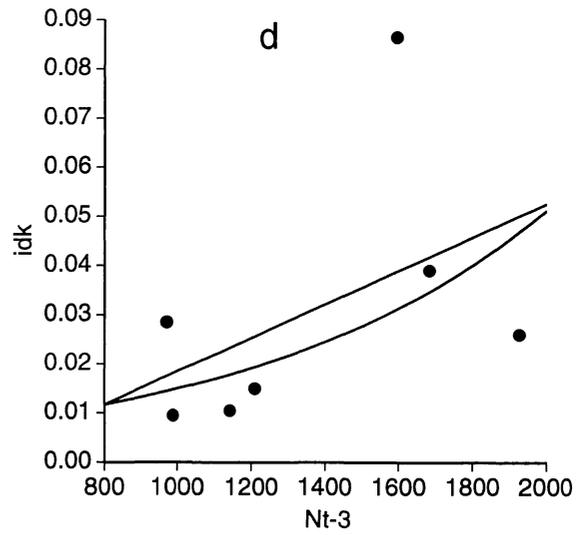
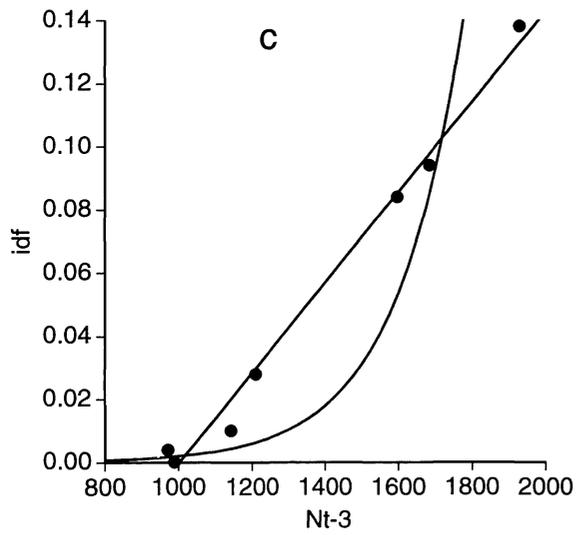
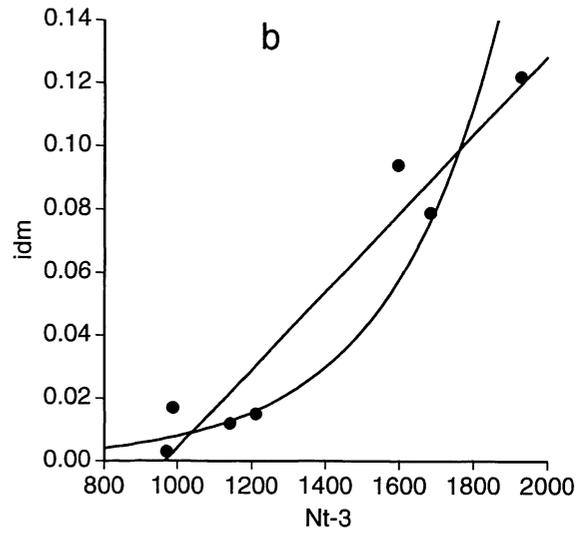
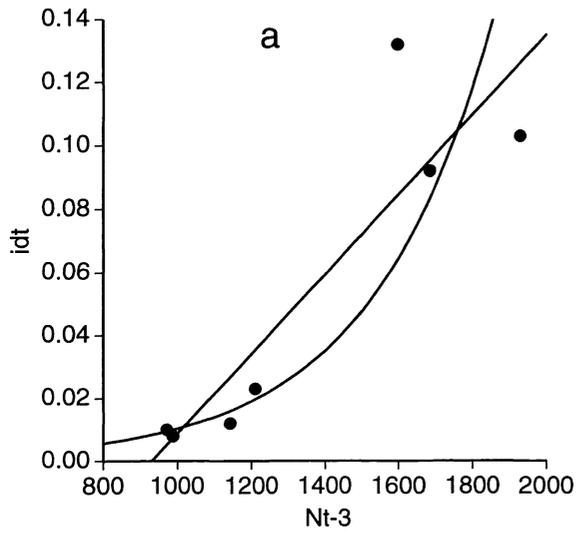
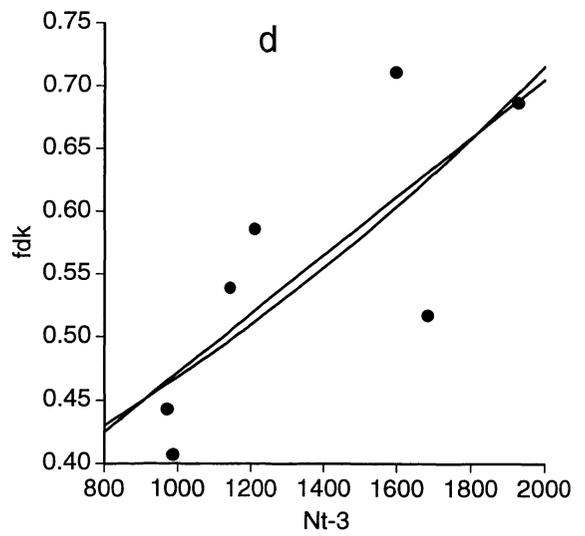
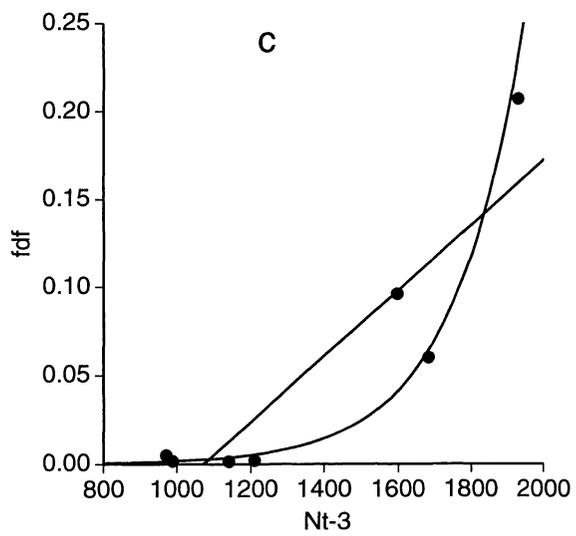
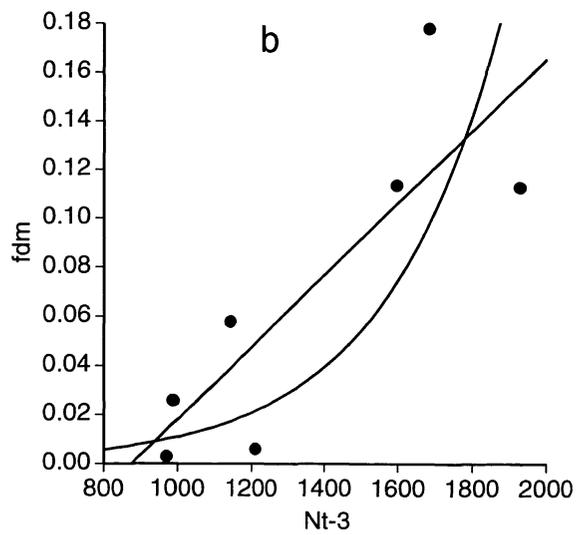
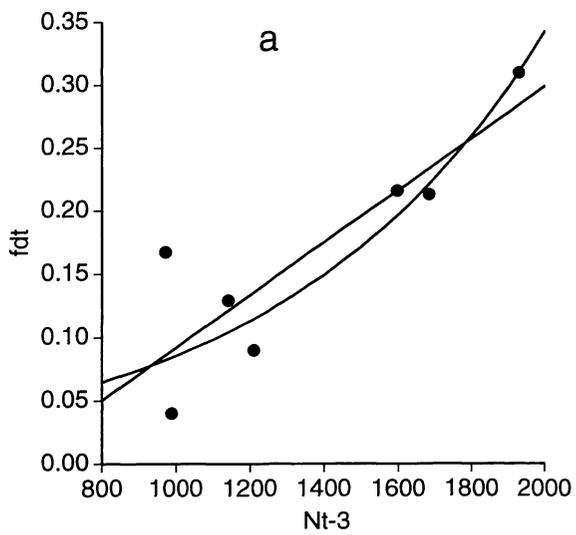


Fig. 4.





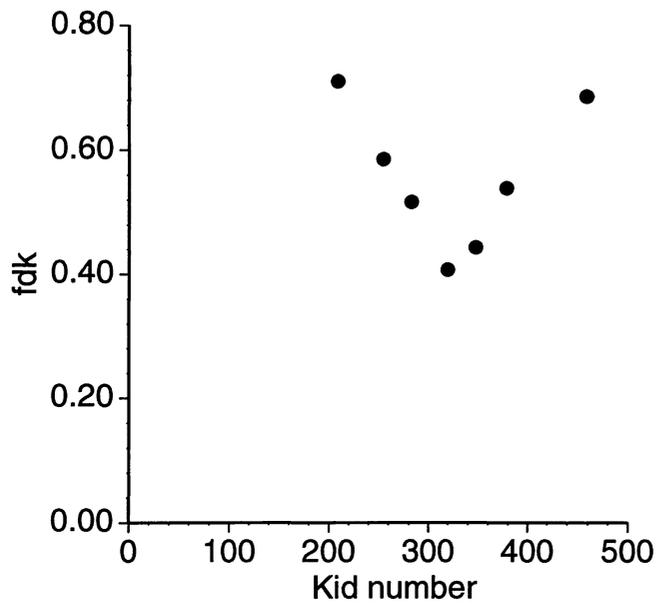


Table 1. Number of Carcasses of *R. rupicapra* found in the Azienda Faunistica di Barbellino-Valbelviso from 1981 and 1989

Year_	Total	Kids	Female 1 or +	Males 1 or +	Undeter.
1981	359	126	132	101	0
1982	83	12	32	21	18
1983	164	12	92	43	17
1984	112	11	44	30	12
1985	131	18	33	25	55
1986	23	4	10	5	4
1987	9	2	1	5	1
1988	14	10	2	1	1
1989	18	3	6	5	4

1 or + : one year-old or older  
 undeter.: undetermined

Table 2. Number of animals hunted of *R. rupicapra* found in the Azienda Faunistica di Barbellino-Valbelviso from 1981 and 1989

<i>Female</i>																
Year	Age															
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
81	3	17	7	9	1	2	2	4	7	7	7	7	4	0	0	0
82	3	9	2	6	4	3	3	2	3	2	5	6	0	0	0	0
83	1	17	10	10	2	1	3	6	6	7	3	7	0	0	0	0
84	19	15	5	7	10	8	5	7	8	6	6	11	0	0	0	0
85	0	4	0	3	0	1	2	0	1	1	1	0	0	0	0	0
86	0	1	0	0	0	0	1	0	0	0	1	1	0	0	0	0
87	1	2	4	3	0	0	1	2	2	1	1	0	2	0	0	0
88	0	20	10	13	10	12	8	7	9	8	6	5	4	0	0	0
89	0	1	2	1	1	1	2	2	1	0	0	2	0	0	0	0

<i>Male</i>																
Year	Age															
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
81	3	16	4	5	8	1	4	2	2	0	0	0	0	0	0	0
82	1	9	7	16	8	15	17	18	11	1	0	0	0	0	0	0
83	5	2	2	3	8	3	8	3	2	0	0	0	0	0	0	0
84	12	5	3	5	10	5	5	2	2	0	0	0	0	0	0	0
85	0	6	10	8	3	3	1	2	3	0	0	0	0	0	0	0
86	0	1	6	5	2	1	2	5	1	0	0	0	0	0	0	0
87	0	4	10	6	2	3	1	4	2	0	0	0	0	0	0	0
88	0	13	4	5	3	3	3	0	1	0	0	0	0	0	0	0
89	0	24	9	15	5	7	4	4	5	0	0	0	0	0	0	0

Tabla 3. Linear regression analysis results for the birth rate and the death rate against the total number of individuals of *R. rupicapra* with different time delays in the *Azienda Faunistica di Barbellino-Valbelviso* from 1981 and 1989

Delay (T)	1				2				3			
	a	b	r <sup>2</sup>		a	b	r <sup>2</sup>		a	b	r <sup>2</sup>	
<i>Birth Rate</i>												
	0.39	-0.05	†	NS	0.46	-0.06	0.20	NS	0.51	-0.09	0.50	NS
<i>Index of Death Rate From Carcasses</i>												
Total Number	-0.05	0.9	0.19	NS	-0.02	0.5	0.16	NS	-0.11	1.2	0.80	**
Males (1 or +)	-0.08	1.1	0.31	NS	-0.04	0.6	0.28	NS	-0.12	1.2	0.93	**
Females (1 or +)	-0.06	0.9	0.27	NS	-0.06	0.8	0.33	NS	-0.14	1.2	0.98	**
Kids	-0.14	1.4	0.30	NS	-0.02	1.0	†	NS	-0.15	0.3	0.22	NS
<i>Finite Death Rate From Census</i>												
Total Number	-0.39	1.6	0.37	NS	-0.08	1.8	0.57	*	-0.11	2.0	0.74	*
Males (1 or +)	-0.09	1.3	0.30	NS	-0.09	1.2	0.48	NS	-0.12	1.4	0.70	*
Females (1 or +)	-0.07	0.9	0.16	NS	-0.05	0.7	0.13	NS	-0.20	1.8	0.82	**
Kids	0.43	1.0	†	NS	0.36	1.4	0.22	NS	0.23	0.3	0.58	*

a: interception of linear regression. b: slope for the linear regression (in 10 e-4). r<sup>2</sup>: coefficient of determination. †: r<sup>2</sup> less 0.1. NS: non significant. \*: significant. \*\*: highly significant