ENDOGENOUS AND EXOGENOUS CONSTRAINTS IN THE POPULATION CHANGES OF WILD BOAR (*Sus scrofa* LINNAEUS, 1758)

ANTONIO UZAL[1] AND CARLOS NORES[2]

1. Avda. Pablo Iglesias, 43, 1º Izqda. 33205 Gijón (Asturias), Spain.
2. Dpto. Biología de Organismos y Sistemas, INDUROT, Univ. de Oviedo, Campus de Mieres, 33600 Mieres (Asturias) Spain. (cnores@correo.uniovi.es)

ABSTRACT

The population dynamics of wild boar (*Sus scrofa*) was studied in a time series over 26 years using data from the Regional Hunting Reserve of Somiedo (northern Spain). This population is controlled by a complex negative feedback system that acts with one (main) and two (secondary) years of delay (lags). The primary feedback might be explained by intraspecific competition for food resulting from fluctuations in mast production (acorns and beech), and the secondary feedback might be explained by the influence of weather conditions or the delay of a cohort to reach reproductive status. We used a stochastic model that takes environmental variability into consideration when testing the demographical analysis that's obtains simulations from real data.

Key words: Cantabrian Mountain Chain, demography, density dependence, Northern Spain, *Sus scrofa*, Wild boar.

INTRODUCTION

The wild boar (*Sus scrofa*) is a very important species from an economical point of view because it is a very popular game species in many countries and a potential (or present) pest (Oliver and Fruzinski 1991) for agriculture (Boisaubert and Sand 1994) and animal health (Coustel 1994). It is quite probable that the species interferes with the conservation of endangered species because of competition, as in the case of brown bear (Nores and Palomero 2000) or predation, as in the case of capercaillie (Klaus and Bergmann 1994). When a population of an economically important species erupts or crashes, an investigation of the underlying cause might be an urgent problem in applied ecology (Pielou 1974). That dual nature requires a management control system. To do that, the knowledge of the wild boar's population dynamics must be improved, as does the need to determine the trends: stationary, positive or negative. Furthermore, the nature of and the reasons for fluctuating densities must be determined. Fluctuating densities are very common phenomena in organisms that

have a delayed response to density-dependent controlling mechanisms, even though the environmental conditions remain stable (Pielou 1974).

On the other hand, the relative importance of density-dependent and density-independent factors in controlling population densities and dynamics is a central issue in population ecology. Much of the empirical work has focused on forest pests (insects) or vertebrates, and has revealed population cycles and it was not until the past decade that non-lagging density dependence was taken into consideration (Turchin 1990). More recently, Saether (1997) tried to test Lack's hypothesis (based on bird population studies) using large herbivores and tried to include both sets of factors in a general hypothesis by suggesting that in a seasonal environment the fecundity rate will be determined in a density-independent way by the amount of resources available for breeding in the favourable part of the year, while in winter intraspecific competition is a major density-dependent regulating factor. Saether (1997) found that both mechanisms are involved and allow for an instable population equilibrium in the absence of predation, but he emphasised the need for very long time series data to test statistically the return tendencies. Saether (1997) used only cervid and bovid ungulates that have a long life-span and lower reproductive potential, and it seems important to test some of his conclusions with a species such as the wild boar, which exhibits demographic plasticity.

In our study, we analyzed the population dynamics of the wild boar using time series data. We quantified population changes featuring oscillations and we aimed to determine the feedbacks that regulate the population and quantified the value of the endogenous (intrinsic capacity of increasing, intraspecific competition) and exogenous constraints (weather conditions) that lead to population changes. We also performed simulations that allowed us to test the model using the present population changes and to test the influence of internal and external forces on the fluctuations in population density.

MATERIALS AND METHODS

Study Area

Population and environmental data were obtained in the Regional Hunting Reserve of Somiedo (Figure 1). This Reserve of 86.000 ha, which is in the northwestern Iberian Peninsula, has an Oceanic-Mountain climate, an elevation between 400 – 2.417 m, an annual average rainfall >1.000 mm, and annual days of snowfall of 5 at 480 m and 23 at 1280 m.
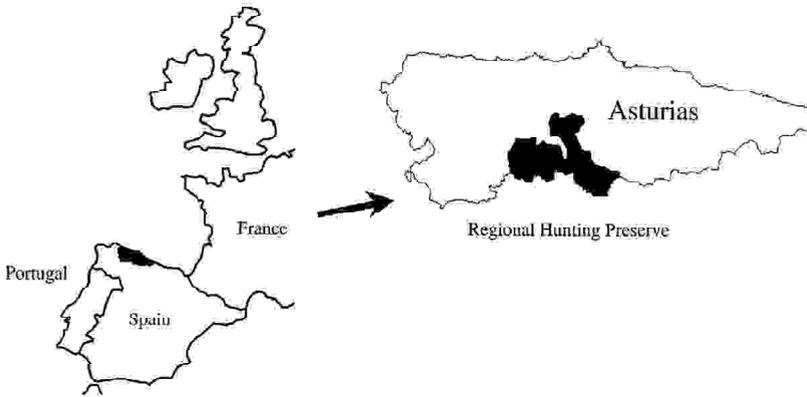
Figure 1. Location of the Regional Hunting Reserve of Somiedo in Northern Spain

Population data

Hunting bag indexes are often used to study wild boar population trends (Tellería and Sáez-Royuela 1985, Sáez-Royuela and Tellería 1986, Neet 1995) or to determine wild boar densities (Sáez-Royuela and Tellería 1988, Boitani et al. 1995). We used the number of wild boars killed per hunting day during the hunting season (from September 1 to January 31, around 70 days per year). This index is really an index of the catch per unit effort, which could be a reasonable representation of the changes in the density of harvesting populations under certain conditions (Caughley 1977), including the following:
   - Conditions of catching are standardized.
   - The catching of one animal does not interfere with the catching of another.
   - Animals must not learn to court or avoid capture. The time series used is from 1968 to 2000, although for some analyses we had to use a shorter, but uninterrupted period (1974-2000; Figure 2).

In the Hunting Reserve of Somiedo, the wild boar hunting system remains quite similar to the original format, but, in 1994, there were some small changes that increased the quota of wild boars hunted, but these changes were considered to maintain an equivalent effort over time. The changes include an increase in the upper limit from three to five animals per day, and the addition of February to the hunting season. We tried to maintain the same catch effort refusing over three individuals shot (less than 8% of the hunted animals) and not considering the results of the additional month.
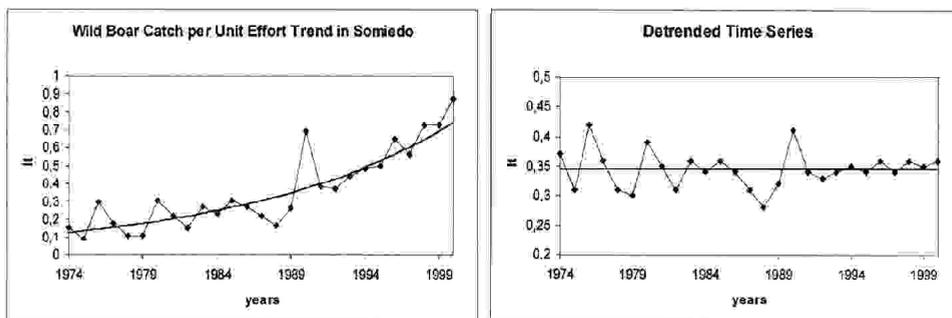
Figure 2. Trend of wild boar catch per unit effort index (I_t) in Somiedo Hunting reserve during
the period 1974-2000 (left) and the same time series detrended (right)

Population parameters

Beginning with the catch per unit effort index (I_t), we calculate the annual multiplication rate and the exponential rate of increase for every year.

- *Multiplication rate* $_t$: The ratio of numbers (or indexes) in two consecutive years

$$_t = I_t I_{t-1}^{-1}$$

- *Exponential rate of increase R$_t$*: The slope of the increase in the *t* year

$$R_t = \ln {}_t$$

Analysis of Population Dynamics (1974-2000)

We used the software program, Population Analysis System (PAS) version 4.0 1994 © Ecological Systems Analysis, developed by Alan Berryman and J. A. Millstein, as a tool to analyse the population dynamics and which we founduseful in choosing models to describe and analyse time series (Berryman 1992, 1999).

Analysis

A positive trend presented a problem because it did not allow some calculations and hid some population characteristics. We transformed our trending time series into a stationary series (detrending series, Berryman 1999) to allow the analysis of population dynamics. The time series was detrended by rotating the data (now I'_t) around the mean (Figure 2).

The PAS program makes, among others, three automatic calculations to analyse the population dynamics and model the results.

The first calculation for the PAS is the Return Time (*RT*), which is the time it takes for a trajectory to return to its mean value after being disturbed. A variance that is slightly longer than the mean indicates an aperiodic or trending series. In a stationary series, the mean of return time acts as an indicator of the order of the dynamic

population feedback, so a value around 1 suggests first order dynamics (time lag one) in the population.

The PAS also calculates the Autocorrelation Function (*ACF*) of stationary time series. This is a method developed by Moran (1953) as a current ecological technique to detect periodic oscillations in time series data. It detects endogenous and exogenous constraints and analyses the reply speed to dominant feedback (Berryman 1999). If periodic cycles occur, peaks with high correlations (positive and negative) can be observed in regular periods. In a non-stationary time series, correlations decline continuously with increasing lag. If the series is stationary, the autocorrelation function is balanced more or less evenly around the zero correlation value. In noisy time series, ACF reveals the periodic pattern if it is present (Turchin and Taylor 1992).

The new automatic calculation by PAS Program is the Phase Portrait (*PP*), a plot of the per-capita rate of increase R on population density (relative I_t, on this case) at lag period d. If the phase plot describes a clear orbit (a rounded distribution of the points) the lag period is too small or too large, but if the points show a relatively narrow orbit, the lag can be calculated by choosing the best correlation with different lag periods. The phase portrait is a useful technique to identify the dominant lag, but also to test whether the simulation arising from the model agrees with the real data. We tested this agreement using the Pearson correlation coefficient to compare the dispersion of the plot and the regression lines in slopes, and in the origin with the Student's *t*-distribution.

Another calculation is the Partial Rate Correlation Function (*PACF*), between the rate of increase R and $\ln I_t$ with different lags with the effects of lower lags removed, to test the effect of density in the growth for each lag. That tool is one of the most useful for determining the order of the dynamics in stationary series (Berryman 1999) because every correlation coefficient is independent of the previous correlation.

Models and simulations

The usual function to describe a population's rate of increase is

$$I_t = I_{t-1} \, \mathrm{e}^R$$

where R is the exponential rate of increase describing the change of a population from one year to the next.

That deterministic model can be changed easily into a stochastic model adding to the R-value a random coefficient Z and a measure of the observed variability, as the standard deviation s of the observed values for every year (including both environmental variability and sampling error). In that case, the initial formula can be substituted by:

$$I_t = I_{t-1} \, \mathrm{e}^{R + sZ}$$

Relationships with Weather Conditions (1968-2000)

The only measured environmental variables available were meteorological factors because other external conditions, such as food availability, were unknown.

To test the relationships between weather conditions and the changes in the wild boar population, a virtual meteorological station was made using four stations with partial data to obtain a complete data set by using multiple regressions from month to month to eliminate the dependence of the dates.

Beginning with 10 basic meteorological variables related to temperature or rainfall in critical months (winter, breeding season, growth of piglets, and so on), we composed up to 23 variables derived from the basics, such as drought, frozen periods, snowfall, which could be correlated with population dynamics.

We crossed those meteorological variables with population parameters that had one, two, or three lag periods to obtain significant linear correlations and one multiple regression with an annual multiplication rate (λ_t)and exponential rate of increase (R_t).

The value from 1990 was considered an outlier (a population growth of 268% in a mammal can be difficult to explain ecologically) and was both included and excluded in the regressions between population parameters and meteorological variables.

RESULTS

Analysis of Population Dynamics (1974-2000)

The time series of the wild boar in Somiedo is obviously non-stationary because it shows a positive trend ($r = 0.8575; p < .001$) with a whole yearly increase over 7% ($R = 0.069;$ $\lambda = 1.072$), without taking emigration into consideration (Figure 2). On a detrended time series (Figure 2), densities oscillate around an equilibrium line in which it is possible to calculate some population parameters that are useful in creating a model, and which is impossible in a trending population.

The mean of the return time (*MRT*) of the original series was 1.52, but their variance was calculated by the PAS program as being infinite, which is characteristic of non-stationary series. When we removed the trend and transformed our time series to an atrending series, the mean of return time was less than two (as in our atrending series, with *MRT* = 1.17), which implies that density-dependent feedback acts within one time period (year), and suggests first order dynamics (time lag 1) in the population.

The autocorrelation function in the natural time series showed a typical trending result with correlations declining continuously with increasing lag periods, and any evidence of periodic cycles could be observed. When we detrended the series, the autocorrelation function is representative of a stationary series showing damped-like oscillations, but it does not have genuine periodic cycles (Figure 3).
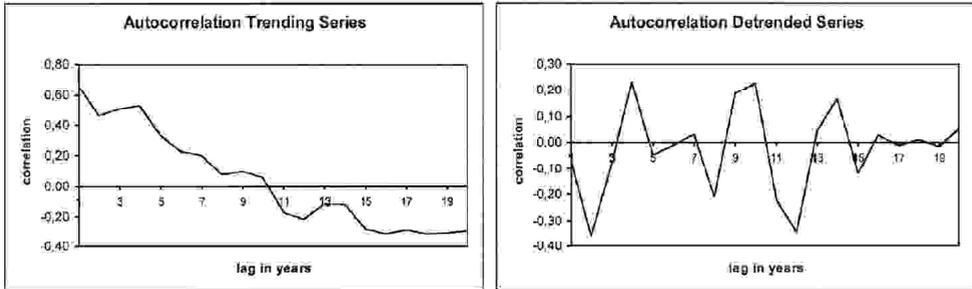
Figure 3. Autocorrelation function in the trending time series (left) and autocorrelation function
in the atrending time series (right)

In detrended time series, we obtained a relative narrow phase portrait and the best correlation came from using a one-year lag. That phase portrait, with many points close to the equilibrium point $R = 0$ (Figure 4) showing a narrow orbit and no obvious direction, is typical of a first-order dynamic system, according to the value of the mean of return time. We can confirm that result by choosing the best correlation for those points that are obtained with a lag of one year ($r = -0.695$), but also noticeable is a second lesser, but not negligible, two-year lag feedback ($r = -0.208$), which we also see in the partial rate correlation function (Figure 5).
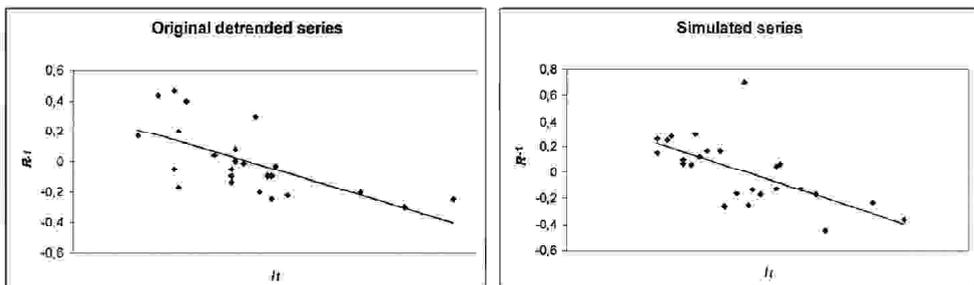

Figure 4. Phase portrait of wild boar from the detrended time series with a lag period of one year (left)
and form a simulation of stochastic dynamic model with one lag period (right)

Simulations

The dynamic behaviour of the model can be studied by simulation. Simulations can be run with no external variability (deterministic model), in which we simulate how the population is stable or whether the dynamics are periodic or chaotic.

In our case, we obtained the best dynamic model by including both negative feedback mechanisms (with one and two years of lag) and obtained the 57.5% of the explained variance (it decreases to 48.3% when considering only the first-order feedback), with a maximum per capita rate of change $A = 0.936$.
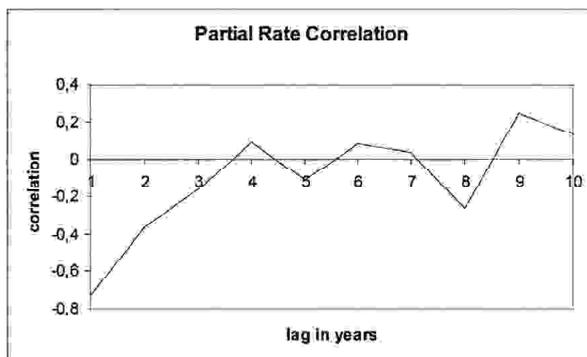

Figure 5. Partial rate correlation of wild boar time series

With that population characteristic, the PAS programme plots a simulation of up 25 years of the deterministic model (standard deviation is zero). In that case, the initial oscillations are damped in a 12-year period (Figure 6), for the interaction between a high potential rate of increase and a relatively rapid response to return to its virtual carrying capacity.
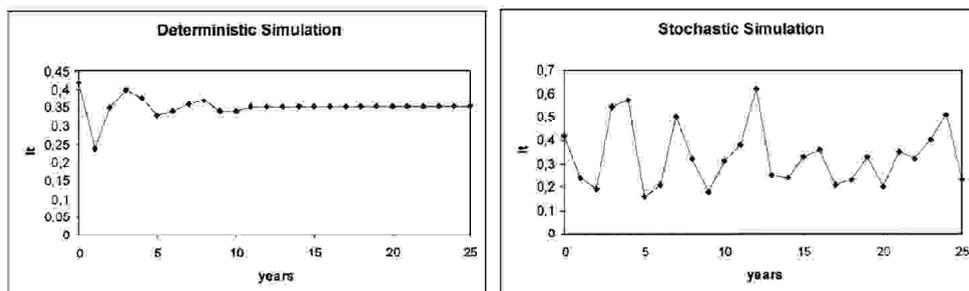

Figure 6. Deterministic Model with two lags and no environmental variability (left) and stochastic dynamic model with two lags using the environmental variation obtained from real detrended data (right)

Using the standard deviation obtained from the model of two-lag multiple regression ($s = 0.3405$), the simulations showed chaotic dynamics (Figure 6), similar to the real data of detrended time series. The model was validated by their phase portrait, comparing whether vectors in both graphs (from real data and simulation)

occupy a similar area and shape (Figure 4). Their correlation coefficients were quite similar (r_r = -0.651; r_s = -0.645) and no significant differences between real and simulated regression lines were found (slope value of t = 1.120; p = 0.252 and origin value of t = 0.132; p = 0.8).

Meteorological Relationships
Trending time series

Using the trending time series, we obtained significant bivariate correlations between "rainy days in a year" and multiplication rate, and exponential rate (Table 1).

When we removed the outlier (1990 data), the results did not improve. We calculated a multiple regression model, but we did not obtain any significant results.

TABLE 1

Meteorological variables showing significant correlation (over 95% level) with exponential rate and multiplication rate of real time series

Growth Exponential Rate R	Days of rain in a year	Pearson's Correlation	-0.512
		Sig. (bilateral)	0.024
		N	19
		Equation	y = -0.0185x+2.7834
Multiplication Rate	Days of rain in a year	Pearson's Correlation	-0.459
		Sig. (bilateral)	0.042
		N	20
		Equation	y = -0.0251x+4.9073

Detrended time series

The detrended time series showed significant correlations with two of the meteorological variables (spring rainy days with a lag of two years and mean summer temperature of the previous year) with exponential rate R and five variables (spring rainy days and number of frozen days, both with a lag of two years and summer rainfall, average annual temperature and mean summer temperature all three of the previous year) with the multiplication rate l (Table 2). All of those determination coefficients are <0.25.

When we calculated a multiple regression with an annual exponential growth rate, the model explains only 27.1% of the variance. The best multiple regression model was obtained with the annual multiplication rate (r^2 = 0.355), including the mean temperature June-August one year before (ST_{t-1}), average annual temperature one year before (AT_{t-1}), and spring rainy days two years before (SR_{t-2}).

$$\hat{l}_t = -0.302\ ST_{t-1} + 0.005188\ AT_{t-1} - 0.410\ SR_{t-2} + 57.149$$

TABLE 2
Meteorological variables showing significant correlation (over 95% level) with exponential rate
and multiplication rate after "detrending".

Growth Exponential Rate R	Spring rainy days 2 years before	Pearson's Correlation	-0.415
		Sig. (bilateral)	0.049
		N	23
		Equation	$y = -0.0627x + 2.9520$
	Mean Temperature June-August 1 year before	Pearson's correlation	-0.441
		Sig. (bilateral)	0.027
		N	25
		Equation	$y = -0.0615x + 10.6738$
Multiplication Rate	Spring rainy days 2 years before	Pearson's Correlation	-0.440
		Sig. (bilateral)	0.036
		N	23
		Equation	$y = -0.5757x + 28.0529$
	Frozen days (Tª 0º C) 2 years before	Pearson's Correlation	0,452
		Sig. (bilateral)	0.035
		N	22
		Equation	$y = 0.3834x - 19.594$
	Rainfall June-August 1 year before	Pearson's Correlation	0.496
		Sig. (bilateral)	0.012
		N	25
		Equation	$y = 0.0090x - 12.521$
	Average annual temperature 1 year before	Pearson's Correlation	-0.446
		Sig. (bilateral)	0.033
		N	23
		Equation	$y = -0,9873x + 113,512$
	Mean Temperature June-August 1 year before	Pearson's Correlation	-0.492
		Sig. (bilateral)	0.013
		N	25
		Equation	$y = -0.9873x + 113.512$

DISCUSSION

The increase in wild boar populations in most of Europe (Tellería and Sáez-Royuela 1985, Sáez-Royuela and Tellería 1986) has been constant in recent decades. That trend hides some of the characteristics of the population dynamics and makes analysis difficult. Therefore, it is useful to perform certain data transformations that allow the use of mathematical tools, which facilitate the analysis.

The autocorrelation function of the trending series of wild boars shot in the Regional Hunting Reserve of Somiedo showed a continuous decline in the correlations when the lag increased because the correlation with previous years is high due to previous density dependence. In the detrended series, correlation coefficients were balanced around zero, but it did not have regular intervals between peaks when lags increase and nor were there any significant autocorrelations. That intermediate *ACF* between damped and random oscillations might represent an interaction between two different forces: one of them trending cyclical or quasi-cyclical (endogenous or exogenous, such as cyclic autumn food availability) and the other chaotic (such as weather). Thus, our wild boar population is characterized by a stochastic exponential growth in the period examined.

The mean return time and the phase portrait obtained with one year lag indicates a dominant time delay of one year, but the partial rate correlation function tells us how multiple feedback is involved; mainly a secondary feedback with a two year delay.

First-order oscillations result from the action of a rapid negative feedback and imply that only one species is involved in population regulation. That might lead to the conclusion that intra-specific competition for food or space is the dominant feedback mechanism. Second-order processes involve delayed negative feedback and imply that mutual interactions between two species are driving the dynamics. That might lead to the conclusion that feedback mechanisms involve also interactions between plants and herbivores or prey and predators (Berryman 1992).

The interactive relationship between the animal population and its resources can fluctuate in a permanent cycle in stable environmental conditions as a result of their endogenous mechanisms (May 1972). Endogenous, density-dependent mechanisms of animals can act as a delayed response as well, caused by the length of gestation and the time between breeding seasons (Caughley 1976), which are usual conditions in terrestrial vertebrates in temperate climates. Depending on the product between the exponential rate of increase *R* and the lagged response *d*, the delayed logistic model theoretically gives dampened oscillations (as in our deterministic model) or cyclic population oscillations (Caughley 1976). Although many regulatory mechanisms might lead to oscillations, this is not often seen in the field, where the fluctuations would become irregular with the influence of other external constraints (Pielou 1974).

The explained variance is an estimate of the relative importance of density-dependent factors in determining the observed dynamics, compared to density-independent factors related to unexplained variance (Berryman and Millstein 1994) because they can act in a chaotic manner. In our model, nearly external density-independent agents probably condition 40% of the variance. Thus, the response to

changes in weather has been considered density-independent factors with one or two year lags in chamois (Capurro et al. 1997) and in the wild boar (Neet 1995).

Modelling the interaction between the population and the factors using the population parameters obtained from the analysis, we can test those diagnostic interpretations. In a constant environment with no external variability, the simulation demonstrated that this population model is damped stable. Refusing regular fluctuations by endogenous causes, we must recognize how the irregular changes are strongly influenced by exogenous random forces, obtaining a stochastic dynamic model very similar to the original detrended series. A probable explanation for the observed variability is that it is caused by environmental stochastic variations, such as food availability or weather changes, as Neet (1995) observed in Switzerland.

The importance of a first-order feedback mechanism in population control suggests that the wild boar population was regulated by fast-acting negative feedback, of which the intraspecific competition for limited resources is the most obvious explanation. It seems contradictory to propose a hypothetical intraspecific competition within a population in an exponential growth, in which unlimited resources are supposed, but if the oscillations depend on environmental stochasticity, an unstable environment could change from limited to unlimited resources from one year to the next. The wild boars from Somiedo are feed naturally and winter survival and successful breeding depend on a very unstable food supply in autumn (acorns and beech-mast) related to other density-independent factors (such as weather conditions) to explain the serrated oscillations in an increasing trend and both multiple negative feedback involved.

In other ungulates, such as deer, density dependent-related changes are reported in terms of changes in age at maturity, in the proportion of adult females conceiving or calving in a given year, and in first-winter mortality of juveniles, being the changes in rates of recruitment the main component of regulation, while density-independent factors affecting population dynamics are usually regarded as destabilizing, rather than regulatory factors, due to stochastic nature of consequent changes in mortality and recruitment (Putman et al. 1996). Clutton-Brock et al. (1997) studied two populations of ungulates (Soay sheep and red deer) living on islands in predator-free environments. They suggested that the contrasting dynamics of these two populations are caused by differences in fecundity and maturation rate. When red deer increase in the population, density depresses fecundity and juvenile survival. In contrast, Soay sheep, which have less flexible reproductive control, grow quickly until the population exceeds winter carrying capacity, which triggers over-compensatory winter mortality in all age classes. The wild boar has very high juvenile mortality (near 69% in the Cantabrian Mountains in their first year of life; Sáez-Royuela 1989), which is higher

than that of red deer on the Isle of Rhum (Lowe 1969), which suggests that regulation might affect younger animals more than the population as a whole. The mortality of young animals might affect population growth with a relatively long lag, until this cohort reaches sexual maturity, but also in a lesser lag, delaying the threshold in body weight for the onset of maturation, which has been frequently demonstrated in wild boar (Aumaitre et al. 1982, Sáez-Royuela 1989, Rosell 1998). Sáez-Royuela (1989) found southward of the Cantabrian Chain a significant correlation between density of wild boar and the number of piglets, with a lag of one year, consistent with our suggestion of primary feedback. But food availability and, as a consequence, competition, is not constant in this area, which makes this population feedback mechanism more complex.

Usually, food availability in a herbivore-plant system is considered to be a self-regulating factor in populations. In the wild boar, however, often food availability depends upon other external factors. Choquenot (1998) found that feral pig populations in Australia show a strong dependence on food availability caused by environmental factors, rather than by the consumption from pigs. In our case, 25% of the area of Somiedo is covered by deciduous forest in which mast production varies considerably among years and, therefore, the variation coefficient shown by oak and beech production ranges from 114 to 138 % (INDUROT 2002). This autumn food is very important to winter survival and successful reproduction of primiparous or even adult female wild boars (Vassant et al. 1994, 1995, Massei et al. 1996). That variability should condition yearly variations of the annual multiplication rate providing *ad libitum* food resources some years and strong intraspecific competition in others, combining one and two years of delayed demographic effects**.** In another area of the Cantabrian Mountain Chain, Sáenz de Buruaga (1995) found evidence of active searching for acorns by wild boars. During the low mast of a low or very low availability of acorns, a notably higher frequency of acorns appeared in their diet than was expected by chance. In the Pyrenees, with a limited and fluctuating availability of food, the wild boar population follows *R*-strategies, while in the closed Ebro Valley, with almost unlimited and stable food resources from intensive agriculture, wild boars exhibit a *k* demography (Herrero 2003). In this fluctuating scenario, a *R*-strategist can obtain the best performance, and reveals a high mortality rate and the capacity to recover from population disasters, as well as high annual demographic growth (which is more similar to hares than to ungulates; Jezierski 1977).

Weather effects on ungulate populations with delays of one or two years are described in wild boar (Neet 1995), British deer (Putman et al. 1996), white-tailed deer and moose (Mech et al. 1987, McRoberts et al. 1995). Our results indicate how meteorological factors can affect annual multiplication rate, not for winter severity,

but for spring and summer conditions (mainly temperature and number of rainy days). Low winter mortality in wild boars was reported in a climate as cold as exists in Poland, where the spring period is least favourable to this species, (Jezierski 1977), but where there is a supplementary food supply. In Asturias, the snow-related deaths of wild boars are the lowest percentage of reported deaths out of hunting in all wild ungulates spread along the region (own data). Also, significant negative correlations between kid production and spring precipitation was reported in Spanish ibex related to perinatal mortality caused by bad weather (Escós and Alados, 1991) and also similar results, related to late spring temperature and summer rainfall, become apparent with red deer (Albon et al. 1994).

Saether (1997) concluded that the population dynamics of ungulates are characterized by a strong influence of density-independent factors, as Choquenot (1998) found in feral pigs, and our results seems to confirm that as well. In our case, the density-independent factors, such as summer weather conditions, are important in the regulation of wild boar populations (although we do not know under which mechanism they function). We also suggest the importance of the availability of acorns and beech mast for wild boar population dynamics, given that it directly affects the fecundity rate and it has an important stochastic component.

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