PRELIMINARY ANALYSIS OF THE TEMPORAL VARIABILITY OF THE ALPINE IBEX POPULATION IN THE GRAN PARADISO NATIONAL PARK

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Abstract - We study changes in size of the population of Alpine ibex (Capra ibex ibex) in the Gran Paradiso National Park, in the Western Italian Alps, by analysing a long series of censuses conducted in the past forty years. Spring and fall counts are shown to be strongly correlated with each other. Spectral analysis of the ibex abundance data indicate two main oscillations, with approximate periods of 3 and 8 years. Meteorological data suggest that the size of the ibex population is limited by winter snow cover.

Résumé - Analyse préliminaire de la variabilité temporaire de la population de Bouquetin des Alpes dans le Parc National du Grand Paradis. Les fluctuations de taille d’une population de bouquetin (Capra ibex ibex) dans le Parc National Gran Paradiso des Alpes Italiennes, ont été étudiées par l’analyse des données recueillies lors de recensements effectués au cours des quarante dernières années. Les résultats démontrent que les décomptes du printemps et de l’automne sont fortement corrélés entre eux. De plus, une analyse spectrale des données permet d’identifier deux oscillations principales dans la taille de la population de bouquetin, avec des périodes approximatives de 3 et 8 ans. Enfin, une analyse des données climatiques démontre que la population de bouquetin est limitée par la chute de neige en hiver.

Key-words: Alpine ibex, Population dynamics, Climatic effects
Mots clés: Bouquetin des Alpes, Dynamique de population, Effets climatiques.

1. Introduction
Ungulate populations appear to be limited by endogenous, density-dependent factors, by the action of predators, and by stochastic factors such as weather (e.g., Picton, 1984; Sinclair, 1989; Skogland, 1991; Grenfell et al., 1992; Escos et al., 1994; Murdoch, 1994; Turchin, 1995; Langvatn et al., 1996; Clutton-Brock et al., 1997; Post et al., 1997; Saether, 1997; Forchhammer et al., 1998; Gaillard et al., 1998). Given this multiplicity of causes and effects, a proper identification of the key factors that affect a given ungulate population is crucial for its sensible management.

The first step to understand the dynamics of a natural population is the quantitative assessment of its temporal variability. Here, we discuss some preliminary results of the analysis of the population dynamics of Alpine ibex, Capra ibex ibex, in the Gran Paradiso National Park (PNGP). As the Alpine ibex population in the PNGP is censused twice a year, we investigate whether there are significant differences between the two yearly censuses. An earlier analysis of the Alpine ibex population of PNGP was presented by Bassano et al. (1992), who detected apparent periodicities in the ibex abundance. In the present paper we

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discuss their results, in light of new analyses of the data set. Furthermore, we consider the possible role of weather in limiting the Alpine ibex population at PNGP.

The Gran Paradiso National Park, located in the western range of the Italian Alps, was founded in 1922 and is the oldest protected area in Italy. The park is located between Piedmont and Valle d’Aosta (Italy), at 45° 25’ N, 7° 34’ E, partially bordering on the Vanoise National Park in France. As a mountain park, the PNGP is characterized by large, scarcely populated areas that are mostly located above the tree-line. Most of the park (42,389 hectares, representing 58.6% of the total park surface) is composed of alpine pastures, moraines and unproductive land. Hunting is forbidden in the park, and human activities are in general limited.

Two mountain ungulates live in the park, the Alpine chamois (Rupicapra r. rupicapra) and the Alpine ibex (Capra ibex ibex). The protection of the Alpine ibex, which were endangered by excessive hunting pressure, was the main reason for creating the Gran Paradiso National Park, formerly a royal hunting reserve. Both ungulates are now fully protected in the park, and the Alpine ibex is protected also outside the PNGP. No predators are present in the park area and thus ibex mortality is due to age, winter starvation and disease.

Alpine ibex live mainly above the tree-line at altitudes between about 2,000 and 3,500 meters, descending to the lower elevations during late winter and spring. Ibex forage on grass, mosses and lichens, and are most active at dawn and dusk. Typically, adult males live separated from the herds of females and subadults. During the mating season, December through January, males fight with each other, in order to gain access to females. Females give birth to one, and rarely two, kids the following June. In general, females first reproduce when three years old. Before this age, young males and females stay with adult females in small herds. Although individuals as old as 20 years have been observed, few ibex survive beyond 14 years.

2. Censuses of the Alpine ibex population at PNGP

During the last forty years, the Alpine ibex population of the PNGP has been censused twice a year, namely in late spring and early fall. Each census has recorded the number of adult males \((M)\), adult females \((F)\), male and female yearlings \((Y)\), and male and female kids \((K)\). The latter were counted only in fall until 1984, and both in spring and fall from 1985 on. Censuses are conducted along trails and from fixed locations within each surveillance area. Each park warden is assigned an average area of about 1,050 hectares. Most of these areas are treeless, making observation easier. This effort has led to a long time series of ibex abundance in the park, which provides important information on the dynamics of this population. Here, we analyze the time series of ibex abundance recorded from 1956 to 1997.

Figure 1 shows the total ibex abundance over the study period, as given separately by the spring and fall counts (here we do not include the kids due to the fact that spring counts for kids are available only for the last 12 years). The total ibex population, \(T_n = M_n + F_n + Y_n\), where \(n\) indicates the year, fluctuated around 3,300 individuals until the mid eighties, when an apparent eruption of the population took place, leading to a peak abundance of about 5,000 individuals. After about ten years, the total number of ibex started decreasing.

Figures 2 and 3 show the abundances in the four age/sex classes discussed above, as given by the spring and fall censuses respectively. During the population increase, the number of newborns and yearlings did not increase significantly, suggesting that the increase in the ibex population was due to higher survival rate of non-reproducing adults rather than to increased recruitment. This interpretation is confirmed by the study of the age distribution in the ibex population, which indicates that there was a larger
Fig. 1 - Time series of the total ibex abundance, as separately obtained from spring and fall counts.

Fig. 2 - Time series of the abundances in the four age/sex classes considered (males, females, yearlings, newborns) as obtained from spring counts.
Fig. 3 - Time series of the abundances in the four age/sex classes considered (males, females, yearlings, newborns) as obtained from fall counts.

Fig. 4 - A comparison of fall and spring counts of ibex in the PNGP for males during 1956-1997.
Fig. 5 - A comparison of fall and spring counts of ibex in the PNGP for females during 1956-1997.

Fig. 6 - A comparison of fall and spring counts of ibex in the PNGP for yearlings during 1956-1997.
Fig. 7 - A comparison of fall and spring counts of ibex in the PNGP for kids during 1985-1997.

proportion of old individuals during the eruption (Bassano et al., 1992). An important question is whether there are significant differences between spring and fall censuses. Figures 4-7 compare the number of males, females, yearlings and newborns counted in the fall with those counted in the previous spring.

In general, fewer adults and yearlings are seen in fall than in the spring. The ratio between fall and spring counts for adults and yearlings is approximately constant, and it is independent of the class (males, females or yearlings). Presumably, the difference between the results of spring and fall censuses for adults and yearlings can be ascribed to a wider dispersion, to areas which may be outside the park, in late summer and early fall. Later in the year, ibex concentrate in the park. Linear regression of the fall versus spring counts gives slopes 0.79±0.03, 0.80±0.04 and 0.79±0.06 for males, females and yearlings respectively, and 0.95±0.13 for newborns. The correlations between fall and spring counts are respectively 0.98, 0.95, 0.94 for adults and yearlings, and are highly significant (Student t-test: p<0.001). This indicates strong correlation between spring and fall counts of adults and yearlings, and it suggests that one count per year is enough to monitor fluctuations in ibex abundance.

3. Spectral analysis

In spectral analysis, a generic time series, $X_n$, $n=1,...,N$, recorded at unit (e.g. yearly) intervals, is decomposed into the sum of different sinusoidal components with period $N/k$, where $k=1,...,N/2$. From this, we can write:

$$X_n = \sum_{k=1}^{N/2} A_k \cos(2\pi \frac{k}{N} n + \phi_k)$$
where $A_k$ is the amplitude of the component with period $N/k$ and $\phi_k$ is its phase. The quantity $|A_k|^2$, where the vertical bars indicate the absolute value, provides a measure of the variance explained by the component with period $N/k$ (see, e.g., Box & Jenkins, 1976). The power spectrum is herein defined as $P(k)=2|A_k|^2/N$ and it provides information on how the variance is distributed among the various components. A significant peak of $P(k)$ at a given period $N/k$ implies the presence of an energetic oscillation with this

Fig. 8 - Power spectra of the total ibex abundance data in the period 1956-1983, as obtained from spring and fall counts.

Fig. 9 - Power spectra of the abundance of adult (males and females) and young (yearlings and newborns) ibex in the period 1956-1983. Ibex abundance is obtained from fall counts.
periodicity in the signal considered.
In the study of Bassano et al. (1992), apparent periodicities of about 8 yr and 3 yr in the ibex abundance were detected. With such a small number of data points, however, power spectra have very low frequency resolution and almost null significance, and must be interpreted cautiously. Moreover, the sudden increase during the last ten years makes the time series strongly non-stationary, leading to spectra that are dominated by low-frequency components (the so-called red spectra, see e.g. Balmforth et al., 1999). For this reason, we have computed the spectra (by a standard Fast Fourier Transform routine) only for the first 28 years of measurement (1956-1983), during which the total population was stationary on average. Figure 8 shows the spectra obtained from this first segment of data, for both spring and fall counts. A Hanning filter has been applied to the power spectrum. Two spectral peaks, at about 8 yr and 3 yr, are apparent, confirming the earlier inferences.
It is interesting to compare the spectra of the total population with those of specific sex-age classes. Figure 9 shows the spectra, for the first 28 years, of the time series of the total number of adults, $M_n+F_n$, and of the total number of yearlings and kids, $Y_n+K_n$, as obtained by the fall counts. A standard Fast Fourier Transform with Hanning filter has again been used. The spectrum of the adult abundance shows strong evidence of an approximate 8-yr periodicity, while there is less evidence of a 3-yr periodicity. Conversely, the spectrum of the yearlings and newborns shows increased spectral power at a periodicity of about 3 yr, and only weak signs of longer periodicities.
Although the indications of the spectral analysis must be regarded as speculation for
such a short series, these results suggest the presence of two different mechanisms, associated with the 3-yr and 8-yr periodicities, affecting different age and/or sex classes.

4. Weather effects on population dynamics

The most striking aspect of the ibex abundance data (Fig. 1), is the sudden increase in the total population during the period 1985-1995. Its cause, then, should be properly determined. First we note that large carnivores, like lynx, have been absent from the study area since the end of the last century, so it is not possible to ascribe the growth of the ibex population to decreased predation pressure. Analogously, hunting has not been allowed in the park since its creation, and thus one cannot invoke a changed hunting pressure on the population. Potential causes may include a decreased impact of diseases, decreased competition from domestic stock, and weather effects. To explore the role of weather, we considered the time series of rainfall intensity, temperature and snow cover recorded daily at two stations, located respectively at Teleccio lake, 1866 meters above sea level, and at Serrù lake, 2240 meters above sea level. The comparison of meteorological data with ibex abundances suggests that the mean winter snow cover $S_n$, as obtained by averaging the snow depth measured at each station from October to May, is probably the most important climatic factor. The value $S_n$ is an average over the months of October, November and December of the year $n-1$ and over the months of January through May of the year $n$.

Fig. 10 shows the time series of the total ibex abundance, as measured in the fall, together with that of the snow cover $S_n$ at Serrù. An anticorrelation is visible, with more ibex seen when the winter snow cover is smaller.

A more detailed quantitative exploration of the possible climatic limitation of the ibex population is in progress, and will be reported elsewhere. Here we just note that the results shown in figure 10 suggest a significant effect of the depth and/or duration of the snow cover on the ibex population. The most plausible mechanism is through weakening and starvation of older ibex during winter months. In winter, Alpine ibex have serious difficulties in finding food, and many reach the end of that season in physically precarious conditions. A higher, or longer, snow cover may thus lead to the death of the more stressed individuals. Starting in the mid eighties, the snow cover was smaller for several years, compared to the previous period. This climatic fluctuation may thus be the ultimate cause of the eruption in the ibex population. Since snow seems to affect survival more than natality, during periods of reduced snow one expects a larger proportion of old animals, as observed during the period 1985-92 by Bassano et al. (1992).

5. Conclusions

Ibex abundance data from the Gran Paradiso National Park indicate a strong correlation between spring and fall censuses. Spectral analysis of the ibex abundance has suggested the presence of two periodicities at about 8 and 3 yr, associated respectively with the adult and kid ibex subpopulations. A preliminary comparison between ibex abundance and meteorological variables suggest an important role of climate as a limiting factor for the ibex population. In such a situation, the ibex population may undergo large-amplitude fluctuations in phase with climatic variability, as observed in the period 1985-95. Further work is in progress to quantitatively characterize the population dynamics of Alpine ibex at PNGP and the role of limiting climatic factors.

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References


