Sex-age structure of a chamois *Rupicapra rupicapra rupicapra* (Linnaeus, 1758) population in the Italian Alps

LUCA CORLATTI

Università degli Studi di Padova, Facoltà di Agraria, Istituto di Entomologia Agraria,
Viale dell'Università 16, I-35020 Legnaro (PD), Italia.

Present address:
University of Natural Resources and Applied Life Sciences
Department of Integrative Biology and Biodiversity Research
Institute of Wildlife Biology and Game Management
Gregor Mendel Strasse 33, A-1180 Wien, Österreich
E-mail: luca.corlatti@boku.ac.at

ABSTRACT – A population of the Alpine chamois, *Rupicapra rupicapra rupicapra* (Linnaeus, 1758) moving between an area where hunting is forbidden and another where hunted is permitted was investigated to determine whether its sex-age structure changed over time, and if so, the possible reasons for these variations. Census data were collected in a study area in the Italian Alps, using a block-count method. Population parameters, such as age structure, sex ratios, birth rates, kid survival and annual increase, were inferred from data collected during the 12-year period from 1993 to 2004; data from legally harvested individuals were used to provide a partial explanation of the structure in 2004. Although the population appears to be increasing in size, this trend is irregular, possibly due to local hunting practices, which were also quite variable over the study period. The positive recruitment of juvenile classes (kids and yearlings) also suggests that the population is increasing; however, the mean annual increase was low: a result not entirely explained by hunting. Therefore, other limiting factors must be acting on the population demography; for example, natural mortality and poaching of adults. This latter explanation is confirmed by the strongly female-biased adult sex ratio (0.40), which cannot be caused by legal harvesting, since more females than males were harvested over the study period. The unusual relative number of adult females might explain the fairly low 'specific' birth rate (70.7%) and the relatively high 'generic' birth rate (35.9%), which refer to the breeding inhibition of younger females and greater kid survival, respectively. Kid survival (63.7%) was erratic throughout the study period, presumably linked to the capricious Alpine climate. None of the demographic parameters showed density-dependence: however, this may be because the density values over the 12 years (5.7 chamois/100 ha on average) were low and insufficient for triggering density-dependence. The current harvesting regime (including both legal hunting and poaching) appears likely to bias sex and age structure and to lower the annual increase of the study population, although the presence of the protected area seems to mitigate these negative effects. Further studies are required to investigate less visible consequences of hunting on the population (e.g. its genetic structure).
Key words: class-age structure, sex-ratio, chamois, *Rupicapra rupicapra*

RIASSUNTO – *Struttura sesso-età in una popolazione di camoscio* Rupicapra rupicapra rupicapra *(Linnaeus, 1758) delle Alpi Retiche italiane.* Gli studi a lungo termine delle popolazioni animali rivestono un ruolo di grande importanza nell'ambito dell'ecologia di popolazione, della gestione faunistica e della biologia della conservazione. Di particolare interesse risulta la comprensione dei fattori limitanti che agiscono sulle popolazioni e ne delineano la dinamica demografica. Nelle popolazioni di grandi erbivori, le fluttuazioni dei tassi vitali, legate a variazioni stocastiche e di densità della popolazione, sembrano giocare un ruolo di primo piano. In tale contesto si inserisce il presente studio, relativo ad una specie di primaria importanza nell'ambito faunistico alpino, il camoscio delle Alpi *Rupicapra rupicapra rupicapra* (Linnaeus, 1758). L'obiettivo è stato quello di delineare lo *status* attuale della popolazione indagata, attraverso la determinazione della sua struttura e di parametri quali i tassi di natalità, la sopravvivenza dei piccoli e l'incremento utile annuo, rapportandoli con la densità di popolazione e le strategie di gestione operate. Per le stagioni 2003 e 2004 è stata indagata la popolazione di camoscio nell'area di studio "Alpe Colina", il cui territorio (2097 ha) rientra nel comprensorio delle Alpi Retiche centrali ed è caratterizzato, da un punto di vista vegetazionale, dalla presenza di boschi di conifere e praterie alpine e, da un punto di vista geomorfologico, da numerosi circhi glaciali ad ampio sviluppo superficiale scavati prevalentemente su rocce acide. Al suo interno, cospicua è la presenza di attività zootecniche. Numerose le specie di fauna selvatica, la cui presenza è favorita dalla Zona di Ripopolamento e Cattura, chiusa alla caccia, che rientra parzialmente all'interno dell'area di studio. Utilizzando la metodologia del *block-census* sono stati raccolti dati relativi alla consistenza e alla struttura della popolazione di camoscio. Parallelamente, indagini "storiche" hanno permesso di raccogliere dati pregressi relativi alle consistenze, alle strutture di popolazione e all'attività venatoria. Da un punto di vista demografico, un *trend* numerico discontinuo sembra testimoniare l'importante ruolo giocato dal prelievo venatorio, la cui intensità è variata molto negli anni. La struttura di popolazione testimonia una tendenza all'accrescimento numerico, con elevato reclutamento delle classi più giovani (piccoli e *jahrling*), in contrasto con valori di incremento utile annuo medio-bassi, che paiono peraltro non imputabili totalmente all'attività venatoria. Altri fattori limitanti potrebbero probabilmente agire in modo cospicuo sulla dinamica demografica: fra questi, *in primis* la mortalità naturale e il bracconaggio che, negli Ungulati, tipicamente agiscono maggiormente a carico dei maschi. A testimonianza di questo depongono i valori di s*ex-ratio* profondamente squilibrati a favore delle femmine, riscontrati soprattutto nelle classi adulte (0,40), e non imputabili all'attività venatoria, che complessivamente ha inciso di meno sui maschi, nonché l'età media degli adulti, significativamente minore nei maschi, la quale confermerebbe una maggiore incisività dei sopra citati fattori limitanti su questa classe. Tale scostamento potrebbe peraltro avere conseguenze negative sia sulla dinamica demografica sia sulla *fitness* degli individui. L'elevata presenza di femmine adulte potrebbe inoltre spiegare il valore medio-basso del tasso specifico di natalità (70,7%) e quello piuttosto elevato del tasso generico di natalità (35,9%), in relazione, rispettivamente, all'inibizione delle femmine più giovani all'accoppiamento e alla maggiore possibilità di sopravvivenza offerta ai piccoli dalle femmine adulte. Quest'ultima presenta valori nella media (63,7%), pur con notevoli variazioni legate probabilmente alle condizioni climatiche annue dell'ambiente alpino. I parametri indagati non hanno presentato relazioni significative con i valori di densità pre-riproduttiva, con parziale eccezione del tasso generico di natalità. La densità peraltro presenta valori complessivamente medio-bassi (5,72 capi/100 ha), tali probabilmente da impedire l'innesco di meccanismi di densità-dipendenza. In sintesi, lo studio condotto ha permesso di delineare lo *status* attuale di una popolazione di camoscio che presenta delle problematiche legate soprattutto alla disparità nel rapporto sessi. Alla luce di questo, emerge l'importanza assunta dalla Zona di Ripopolamento e Cattura, in grado di mitigare l'impatto antropico sulla popolazione, garantendone la presenza e la vitalità, il ruolo giocato dall'impostazione dei piani di prelievo e la necessità di un attento controllo dell'attività di bracconaggio.

Parole chiave: struttura di popolazione, sex-ratio, camoscio, *Rupicapra rupicapra*

Introduction

The long term studies of animal populations are of great importance for population ecology, wildlife management and conservation biology (Gaillard *et al.* 1998). One of the central themes lies in the understanding of what factors regulate population growth, and how they operate and interact. In large herbivores, vital rates fluctuations in response to stochastic environmental variations and population density play a key-role, and for ungulates, in addition, anthropogenic pressures such as harvesting are of great importance in shaping populations' destiny (Langvatn & Loison 1999). Hunting regime may involve, in fact, a broad spectrum of consequences on populations, both direct, like changes in size and sex-age structure and indirect, like changes in demographic processes (Solberg *et al.* 1998). Therefore, the knowledge of populations' demographic basics, as well as their linkages with the adopted management, assumes great significance in the light of conservation strategies. Managers should thus evaluate the potential consequences of hunting plans on populations' life history, a knowledge that relies on the availability of long-term datasets. Despite its importance within the Alpine faunistic context for ecological, social, tourist and hunting reasons, the scientific contributions regarding the chamois *Rupicapra rupicapra rupicapra* (Linnaeus, 1758) are, in Italy, quite limited if compared with the broad distribution of this species (Apollonio 2004). In particular, little is known yet about its dynamics: most of the studies were carried out in France (see for example Pflieger & Bauer 1986, Poubelle *et al.* 1989, Gaillard 1993, Allaine *et al.* 1990, Levet at al. 1995, Gonzalez & Crampe 2001, Loison *et al.* 2002), very little indeed in Italy (Pedrotti 1989, Tosi *et al.* 1996, Capurro *et al.* 1997, Rosà *et al.* 1997). The proposed study becomes part of this context, as I investigated some aspects regarding the structure of an Alpine chamois population in the Central Retic Alps (Italy), moving between a protected core area and a hunted area (pers. observ. on individually recognizable animals). I combined a 12-year dataset with harvesting strategies, to investigate the modifications in age-sex structure and vital rates (birth rates, kid survival and annual increase) due to anthropogenic pressures (hunting). Moreover, I assessed the importance of population density on the above parameters assuming the occurrence of time lags in affecting them. Therefore, this study aims to explore the effects on the above population in terms of age structure, sex ratio and demographic parameters due to the current harvesting regime. Such knowledge is required for the proper management of the study population.

Materials and methods

STUDY AREA AND CHAMOIS POPULATION

The research was carried out at "Alpe Colina", located within the Central Retic Alps mountain range (Province of Sondrio, Lombardy Region, Italy). It covers 2098 ha, from 1600 to 2669 m a.s.l.. A ridge, going from NW to SE, identifies two sides, one with northern exposure and one with southern exposure. From a geo-morphological point of view, the north side is mainly characterised by softer slopes, and in both sides several glacial circuses are present. The lithological substratum is mainly acid. The vegetation is, in the lower part, dominated by coniferous forests, while the upper part is characterised by the presence of *Caricetum curvulae* (north face) and *Festuce-tum variae* (south face) grasslands. CREDARO & PIROLA (1975) report monthly mean temperatures of about -6°C and +10°C in January and July, respectively and yearly average rainfalls of about 1100 mm. Three ungulate species inhabit this area: Alpine chamois, roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*). Among predators, one golden-eagle (*Aquila chrysaetos*) pair and red foxes (*Vulpes vulpes*) have been often observed. The alpine marmot (*Marmota marmota*) is abundant, especially near houses. Cattle are kept in both sides during July and August. The study site encloses a protected core area (624 ha), where hunting is not allowed. A chamois population within the study area was present at least up to the 1950's, but was afterwards decimated by poaching. That one inhabiting this area, about 142 chamois in 2004, can be considered an almost isolated population and originated, mainly, from 18 animals released between 1985 and 1987. It was then reinforced thanks to another reintroduction (3 chamois) in 1992. In the course of reintroductions, from 1984 to 1993, hunting was forbidden even outside the protected site.

DATA SAMPLING

Census data covering a 12-year span, from 1993 to 2004, were used to infer density and structural parameters of the "Alpe Colina" chamois population. These data were collected using a block-census methodology, consisting of direct animal observation and identification from vantage points. Sex and age classes (kids: <1 year; yearlings: 1 year; subadults: 2-3 years; adults: 4+ years) were assessed referring to behavioural and morphological characteristics (BUBENIK & SCHWAB 1975). The block-counts might lead to numerical underestimation and uncertainties, as far as the sex-age structure determination is concerned (see HOUSSIN *et al.* 1994). In order to reduce misidentification, mainly due to landscape heterogeneity and double counts, annual counts were carried out simultaneously by gamekeepers located at most suitable observation points (strategic points). Counts were performed every year, in July, just after parturition and before hunting season, for about 4 hours following sunrise, when chamois activity is greatest. Censuses were achieved with this standardized pattern for the whole 12-year span. Over 2003 and 2004 males were re-counted during rutting time, to avoid underestimations due to behavioural reasons. The collected data can thus be considered a useful tool for detecting both sex-age structure and demographic basics of the "Alpe Colina" chamois population. Moreover, data concerning hunting activity (n° of harvested animals, their age) from 1993 to 2004 have been used.

EXPERIMENTAL DESIGN

This study required the determination of a number of parameters: population size, age structure and sex ratio (male:female); 'specific' birth rate [100*(n° kids/n° females 2+ years)], 'generic' birth rate [100*(n° kids/total n° individuals, kids excluded)], kid survival {100*[(kids in summer t)-(yearlings in springtime t+1)]/(yearlings in springtime t+1)} and annual increase {100*[(individuals in springtime t+1)-(individuals in springtime t)]/(individuals in springtime t)}; density (n°chamois/100 ha) and hunting data (number and mean age of hunted animals). The outcome of structural parameters investigation has been related to both density and hunting management.

STATISTICAL ANALYSES

To compare both pre-reproductive population age structures and sex ratios over the period 1993-2004 I used the chi-square test (χ^2, PEARSON 1900, in SOLIANI 2004), with a probability level at 0.05. The Mann-Whitney U-test (MANN & WHITNEY 1947, in SOLIANI 2004) was used to compare male and female numerical series between 1993 and 2004. Regarding the population structure at 2004, χ^2 tests were used to investigate whether the sex ratios significantly differed from the expected 1:1 proportion and differences with the 'theoretical' age structure proposed by STRINGHAM & BUBENIK (1975), inferred from an Austrian chamois population considered being stable (i.e. at its equilibrium level). Differences in birth rates, kid survival and annual increase were investigated performing, again, χ^2 tests. Regarding hunting data, as the mean age of hunted animals can be an index of hunting pressure (lower mean age often responds to greater hunting pressure, even though it might be affected by wrong management), it was investigated performing Kruskal-Wallis H-test (KRUSKAL & WALLIS 1952, in SOLIANI 2004). Then, male and female mean ages were compared using the z-test. To test for density dependence of structural parameters, the best would be to perform experiments (CAPURRO *et al.* 1997); however, large Mammals are not suitable for such procedure and, therefore, statistical analysis is the commonest approach. To estimate the effect of density on estimated parameters, linear regressions

were performed; in particular, assessing the importance of delayed density dependence, I performed linear regressions between demographic parameters at year T and density level at year T-t, with t assuming values between 0 and 3. I then searched for the regression with greatest r² value and checked its significance with F-test (FISHER 1925, in SOLIANI 2004).

Results

SIZE
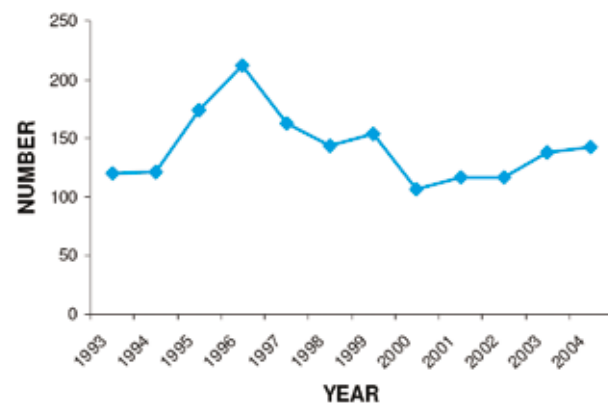The pre-reproductive numerical data are reported in fig. 1.

Fig. 1 *census data of the chamois population at Alpe Colina study site over the period 1993-2004*

After an increase between 1994 and 1996, the population showed a numerical decrease until 2000. Afterwards, it restarted increasing roughly constantly, though with lower rate. In 2004 the pre-reproductive size was about 142 chamois.

SEX-AGE STRUCTURE
The comparison among pre-reproductive populations over the period 1993-2004 showed significant differences in sex and age structures (χ^2=122.475; d.f.=55; P<0.01). However, since the great number of degrees of freedom (d.f.) might have challenged the result, I compared the mean age structures of three distinct phases above: increase '93-'95, decrease '97-'99, increase '01-'04 (intermediate years were excluded). There emerged significant differences between '93-'95 and '97-'99 structures χ^2=19.583; d.f.=5; P<0.01), as well as between '97-'99 and '01-'04 structures (χ^2=20.847; d.f.=5; P<0.01); moreover, significant difference between '93-'95 and '01-'04 structures was detected (χ^2=13.819; d.f.=5; P<0.05). In particular, over the period '93-'95 emerged a greater percentage of adults and a lower

percentage of subadults, in comparison to the period '97-'99. Besides, the '97-'99 period, in comparison with the period '01-'04, showed higher percentage of subadults and lower percentage of adults. Thus, over the increasing phases occurred a greater recruitment of adults. Vice versa, during the decreasing phase a greater number of subadults were recruited. Instead, the percentages of yearlings didn't show any significant difference (fig. 2).
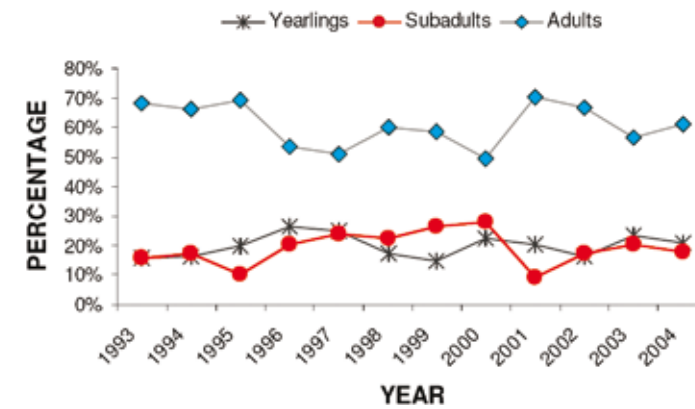

Fig. 2 *percentages of yearlings, subadults and adults from 1993 to 2004 for the study chamois population*

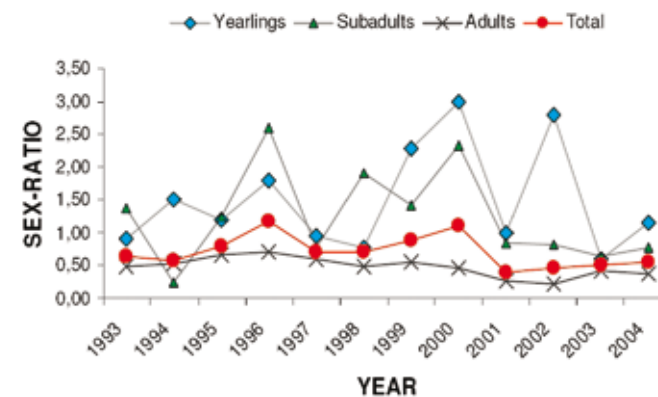The sex ratios values from 1993 to 2004 are represented in fig. 3.

Fig. 3 *sex ratios values from 1993 to 2004 for the study chamois population*

The comparison of yearling sex ratio didn't show significant values (χ^2=17.165; d.f.=11; P>0.05) and its mean was 1.50 (S.D.=0.80). On the other hand, sex ratio comparison over time was significant in subadults (2-3 years) (mean value=1.25; S.D.=0.72; χ^2=27.354; d.f.=11; P<0.01), adults (4+ years) (mean value=0.48; S.D.=0.15; χ^2=22.662; d.f.=11; P<0.05) and for the overall population (mean value=0.71; S.D.=0.24; χ^2=40.017; d.f.=11; P<0.01). The comparison between male and female numerical series over the period 1993-2004 (fig. 4), performing the Mann-Whitney U-test, showed significant difference (nm=12, nf=12; U=2; P<0.05).
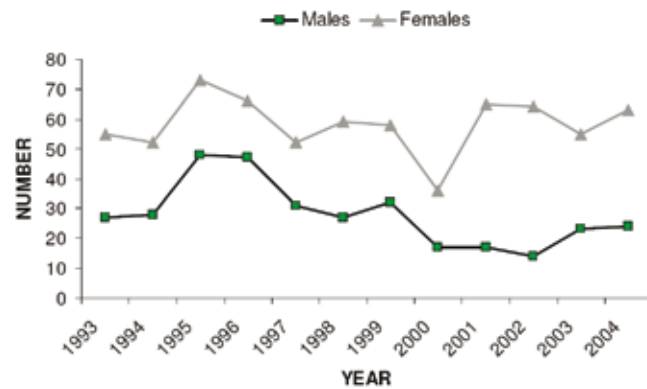

Fig. 4 *male and female numerical series over the period 1993-2004*

With reference to the population age structure observed in 2004, the comparison with the theoretical structure proposed by Pedrotti (1989, based on Stringham & Bubenik 1975) (tab. I) showed a significant difference (χ^2=14.445; d.f.=3; P<0.01: in particular, the observed structure gave evidence for greater recruitment of young classes (kids and yearlings) and lower percentages of subadults and adults.

Age classes	Percentages	
	observed	theoretical
kids	26.7 %	18.0 %
yearlings	16.2 %	12.0 %
subadults	13.9 %	18.0 %
adults	43.2 %	52.0 %

Tab. 1 *comparison of age classes percentages between the study population (observed) and an Austrian chamois population considered being stable (theoretical)*

Moreover, a finer analysis of the observed population (fig. 5) highlighted differences in sex ratios: going from kids (which are assumed to have an unbiased sex ratio, see Levet *et al.* 1995) up to adults, the proportion of females drastically increases. While both yearling sex ratio (0.82) and subadult sex-ratio (0.71) didn't differ significantly from the expected 1:1 proportion (yearlings: χ^2=0.581; d.f.=1; P>0.05; subadults: χ^2=1.528; d.f.=1; P>0.05), the adults showed significantly biased sex ratio (0.40) toward females (χ^2=30.552; d.f.=1; P<0.01).
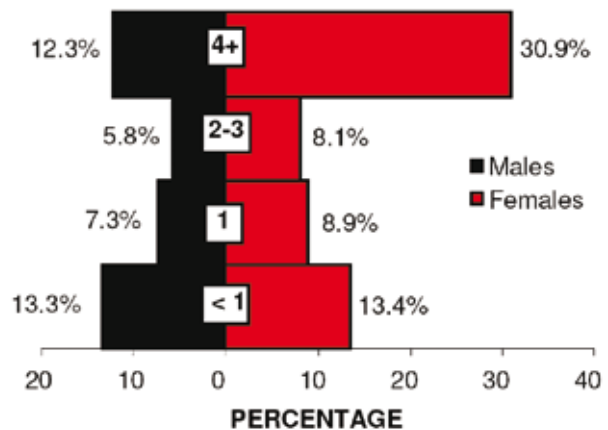

Fig. 5 *sex-age structure of the study population in 2004 (kids:<1; yearlings:1; subadults: 2-3; adults: 4+)*

The overall sex ratio (0.53), as well, resulted significantly biased toward females (χ^2=26.414; d.f.=1; P<0.01).

BIRTH RATES
The comparison of 'specific' birth rate [100*(n° kids/n° females 2+ years)] over time was not significant (χ^2=10.840; d.f.=11; P>0.05) and its mean value was equal to 70.7% (S.D.=5.4%) (fig. 6). The comparison of the 'generic' birth rate [100*(n° kids/total n° individuals, kids excluded)] over time, also, was not significant (χ^2=13.028; d.f.=11; P>0.05) and its mean value was 35.9% (S.D.=6.6%) (fig. 5).
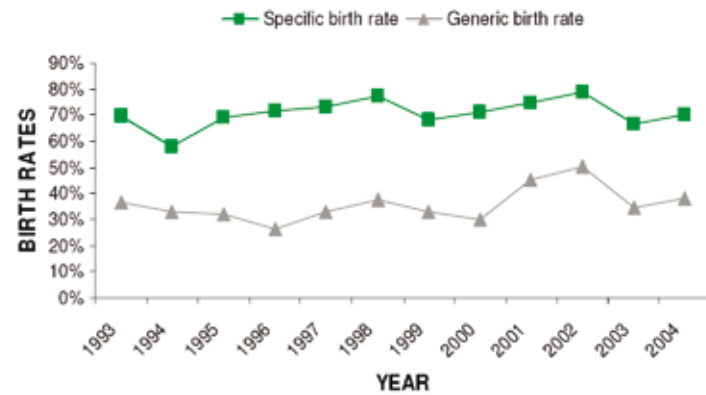
Fig. 6 *'specific' and 'generic' birth rate values over the period 1993-2004*

KID SURVIVAL

As regards kid survival, the comparison of its values over time turned out to be significant (χ^2=100.315; d.f.=11; P<0.01), and a mean value of 63.7% (S.D.=22%) was reported (fig. 7).
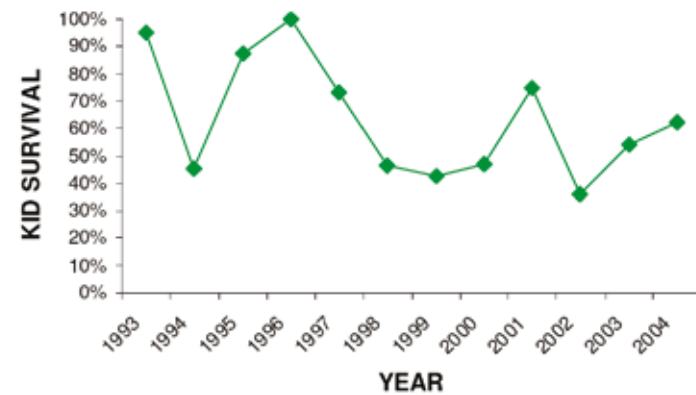

Fig. 7 *kid survival values over the period 1993-2004*

ANNUAL INCREASE

Over the period 1993-2004, the rate of annual increase showed a great variability (fig. 8), as confirmed by the chi-square test (χ^2=233.758; d.f.=11; P<0.01). Its mean value was equal to 5.7%, and characterized by great standard deviation (21.4%).
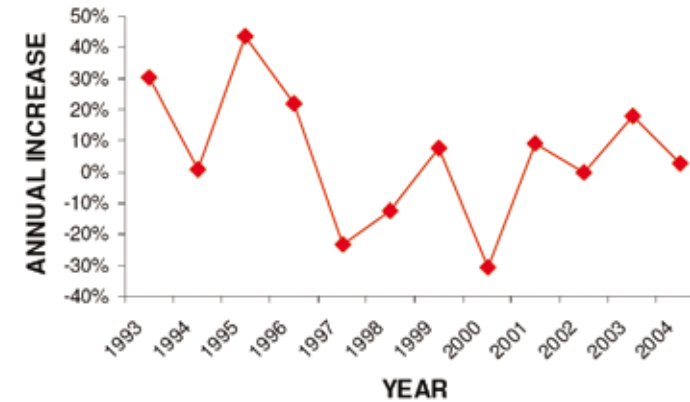

Fig. 8 *annual rate of increase over the period 1993-2004*

In 1995 the population got an annual increase of 40%, which is not possible to occur with chamois, and was likely due to an overestimation came about in the same year.

DENSITY

The pre-reproductive densities from 1993 to 2004 are reported in fig. 9. Obviously, the density trend reflects the numerical one (fig. 1): after an increasing phase occurred between 1994 and 1996 (10.1 chamois/100 ha were then assessed), densities decreased between 1996 and 2000. Afterwards, they restarted increasing roughly constantly, even though with lower rate, and settled around 6 chamois/km².
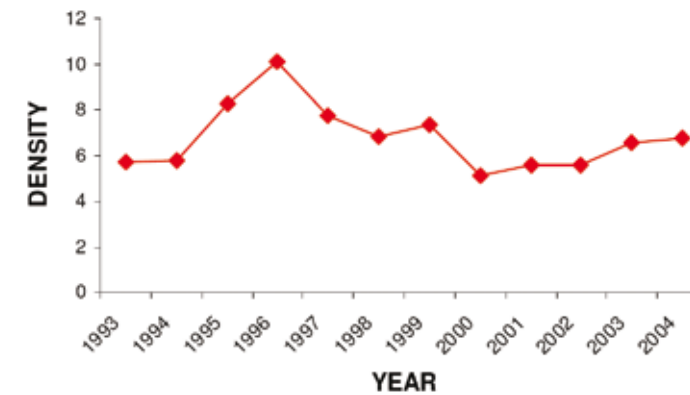

Fig. 9 *density levels (n° chamois/100km²) from 1993 to 2004*

Linear regressions between pre-reproductive densities and demographic parameters (considering an up to 3 years delay) didn't show any significant result.

HUNTING MANAGEMENT
The yearly average hunting incisiveness has been so far equal to the 7.4% of the pre-reproductive population. Every year, over the period 1993-2004, 89.5% of the fore-seen individuals were harvested, as an average. Between 2000 and 2001 there was a drastic decrease of the foreseen chamois to be harvested, then followed by a slower increase. Over the 12-years span, 125 individuals were harvested: 48 yearlings (22 males, 26 females), 27 subadults (16 males, 11 females), 50 adults (23 males, 27 females). Between 1993 and 2000, a greater number of males were hunted, vice versa occurred from 2001 (fig. 10). On the whole, more females than males were harvested so far from 1993 (64 females, 61 males), although the difference is modest.
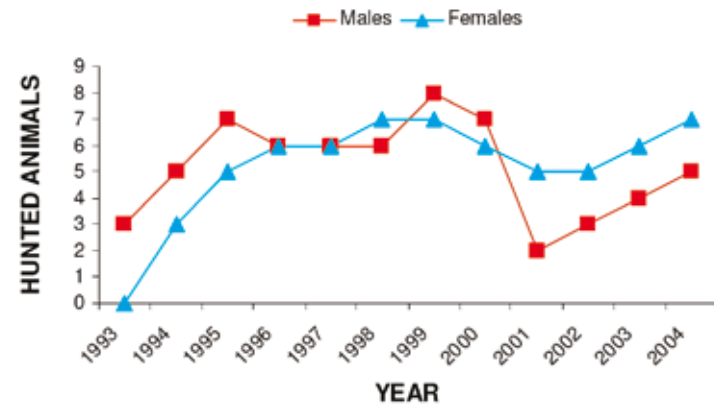

Fig. 10 *number of male and female chamois hunted from 1993 to 2004*

The variation in mean ages of hunted adults is reported in fig. 11. The mean value over the whole period was 7.74 years (S.D.=3.469).
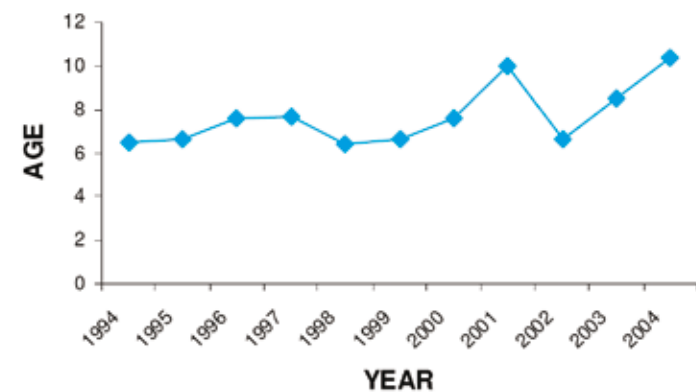

Fig. 11 *temporal variation of hunted adults mean age (n=50)*

The Kruskal-Wallis test didn't detect any significant variation over time (χ^2=6.436; d.f.=10; P>0.05), which might give evidence for a roughly constant hunting pressure. It is rather interesting to give prominence to the differences between male and female mean ages. As a matter of fact, over the period 1993-2004, the male mean age was equal to 5.6 years (S.D.=1.9), significantly lower than female mean age, 9.3 years (S.D.=3.6) as pointed out by the z-test (z=4.5; P<0.01).

Discussion

SIZE
The increase between 1994 and 1996 seems to be fairly too high with respect to chamois physiological features, as the number of individuals raised from 121 up to 212. Likely, overestimation occurred in 1996. The decrease between 1997 and 2000, even though amplified by the previous overestimation, might be due to the great hunting pressure occurred during those years: as a result, the following hunting plans were needed to be numerically reduced.

AGE STRUCTURE
Age structures over the period 1993-2004 showed great differences over time, likely due to the irregular trend above. This might be confirmed by comparisons among mean age structures of the three analyzed phases: in fact, the greater difference detected between mean structures '93-'95 and '97-'99 than the one detected between mean structures '93-'95 and '01-'04 is aligned to the corresponding trends, both increasing, though with different rates. The lower recruitment of adults during the decreasing phase might be linked to greater hunting pressure on this class, while the higher recruitment of subadults during the decreasing phases might find several explanations: on the one hand, it could be direct consequence of adults decrease. On the other hand, other limiting factors, apart from hunting, could have weighed on subadults; among them, emigration: during the increasing phase, the greater percentage of adults might have induced subadults to leave the population. Vice versa may possibly have occurred during the decreasing phase. With reference to the population structure in 2004, there emerged a great recruitment of younger classes (kids and yearlings), typical of populations with a rising trend ("pyramid with broad basis") (CASANOVA *et al.* 1993). Such a situation was often pointed out in hunted populations (POUBELLE *et al.* 1989, FESTA-BIANCHET 2003).

SEX RATIO
As regards overall sex ratio, its change over the period 1993-2004 was mainly due to subadults and adults, as the yearling sex ratio didn't show any significant variation. This might suggest a progressive increase in limiting factors pressure according to the age. The Mann-Whitney U-test showed a significant numerical bias in

favour of females over the 12-year span, as already detected by Levet *et al.* (1995). The overall sex ratio in 2004 (0.53) was heavily biased in favour of females: in natural conditions its value is commonly accepted to vary between 0.71 and 0.83 (Corti 2002). The biased sex ratio toward females is, however, quite a common fact within ungulates since it should be a direct consequence of higher male mortality, higher male migration, higher female fidelity towards their home range (Clutton-Brock 1991; Levet *et al.* 1995, Toïgo & Gaillard 2003) and differences between the two sexes in social behaviour and spatial use (Garin & Herrero 1997). Besides, the sex ratio might be affected by the adopted census methodology (Levet *et al.* 1995), since males inhabiting forests are difficult to count: however, because in this research, in the course of 2003 and 2004, males were counted during rutting time, underestimations have been presumably strongly reduced. Other factors limiting the presence of males might be, of course, hunting (Festa-Bianchet 2003). Weber (2001) reported that, with regards to a population of the French Alps (Salève, Haute-Savoie), protected in 1976 and then hunted in 1977, the overall sex ratio over this biennium shifted from 0.83 to 0.29. Poubelle *et al.* (1989), within a hunting area in France observed the same value (0.29), which strongly contrasted with the ratio observed within a close protected area, equal to 0.72. Parc National de la Vanoise (1983) showed that, within a protected area, the sex ratio was approximately equal (1:1), while within a non-protected area it lowered close to 0.33. In the study population, the 0.53 value might have been the resulting of several factors, such as hunting, poaching, greater male emigration and natural mortality. Even though there was no availability of data concerning this factor, emigration is likely not to play such a great role in shifting heavily the sex ratio toward females because, as already pointed out by Parc National de la Vanoise (1983), the hunting pressure outside protected sites might obstruct dispersal. Besides, since the hunting pressure weighed mainly on females so far, most likely the factors limiting male presence might be identified, principally, with natural mortality and poaching (of which there was some evidence during the study). The biased overall sex ratio was mainly affected by adult sex ratio (0.40), as yearling and subadult sex ratios did not differ significantly from the expected 1:1. Because adult males were not supposed to show high emigration rate and greater number of females was harvested so far, most likely the presence of adult males was limited, mainly, by natural mortality and poaching. This confirms what quoted above and, since the adult sex ratio shifting was substantial, because it affected the overall sex ratio, I might hypothesize that the main factors limiting male presence within the study population were indeed natural mortality and poaching, which acted, principally, through adult males' limitation. Further studies are required to point out the respective roles of such limiting factors. Nevertheless, collecting proper data regarding the study population would be a keystone for its management, since the biased sex ratio toward females might involve several consequences (i.e. in terms of kid mortality and male fitness, see Stringham & Bubenik 1975).

Birth rates

The 'specific' birth rate (n° kids/n° females 2+ years) over the period 1993-2004 showed a mean value of 70.7%. This rate is commonly accepted to vary between 50 and 95%, according to density. Weber (2001) quoted 70% value for high density population, while colonizing populations (low densities) showed values around 90%. In France, 80 and 86% values of specific birth rate were found in colonizing populations by Levet *et al.* (1995) and Parc National de la Vanoise (1983), respectively. Thus, the 70.7% observed in the study population is slightly under the average. However, the explanation for such a value may perhaps be related to something else, rather than density level. The abundance of adult females could, in fact, inhibit younger females from mating and, thus, determine an increase in the age of first parturition. On the other hand, environmental limiting factors might lower subadult females' reproductive success. The specific birth rate density dependence is actually rather controversial (see Allaine *et al.* 1990 and Garin & Herrero 1997); this is not surprising, since it's the survival from kid to yearling that should be most affected by population density (in addition to a later age of primiparity) (Gaillard *et al.* 2000). The χ^2 test run for the study population did not detect for any change over time, which might testify density independence. Such a result would be confirmed by the performed linear regressions. Therefore, it is not easy to understand whether the birth rate value 70.7% was linked to a feeble tendency to increase (density dependence) or, rather, could be read as an intrinsic characteristic of the study population (density independence). Further studies are required to clarify this aspect. A hypothetical scenario might be to assume the specific birth rate to be density dependent, and its values to be relatively interpreted: namely, a great specific birth rate shouldn't necessarily indicate a rising trend, as well as its low value shouldn't indicate feeble increase, because it may be affected, for instance, by biased sex ratio. Rather, to understand the real meaning of observed values, it would be proper to compare them to other values, obtained from the same population at different density levels. This could be, on the other hand, quite problematic since changes in density would likely be accompanied by changes in structure, which, thereby, will affect birth rate value. Bonenfant *et al.* (2005) pointed out how using young:female ratios (in red deer) may possible be misleading (especially in closed habitats) in inferring population dynamics. They give evidence for a great variability over time of this parameter, likely due to both calf survival and mother-young relationship. Given that the young:female ratios were assessed during summer (July-September, period over which kid mortality is assumed to be rather low) and that the study population tends to inhabit open habitats, I may assume the 'specific' birth rate to be a useful tool for inferring the population dynamics. However, I cannot exclude that such temporal variation may even occur with chamois. Thus, further study are required to assess the reliability of young:female ratios as a proxy for birth rate. A finer scale approach to population monitoring (i.e. with marked animals) would be preferable. Regarding the 'generic' birth rate (n° kids/total n° individuals, kids excluded), the study population showed mean value of 35.9% (S.D.=6.6%). As

for the specific birth rate, it seems to be density-independent (CAPURRO *et al.* 1993, in MUSTONI *et al.* 2002) and usually varies between 20-24 and 30% (MUSTONI *et al.* 2002). TOSI *et al.* (1996) found a generic birth rate between 20 and 24% for a colonizing population on the Monte Baldo (Italy). Thus, the observed value is considerably greater than those quoted above, in agreement with values found by PEDROTTI (1989), 31%, and TOSI G. (unpubl. data), 38%, both within a population of the Orobic Alps (Italy). As for the specific birth rate, the χ^2 test didn't detect any significant variation over time, and linear regressions didn't give evidence for density dependence. As regards relationships between specific and generic birth rates, the high value of generic birth rate might indicate a great post-natal kid survival, most likely linked to the biased sex ratio in favour of adult females, more experienced and thus more capable to guarantee kids' survival. Besides, such a great adult female presence might inhibit subadult females mating, and thus lower the specific birth rate value.

KID SURVIVAL

The observed mean value (63.7%) is in line with the existing literature, since the kid survival is commonly accepted to vary between 50 and 70% (PEDROTTI & TOSI 2001, CORTI 2002). FORSYTH & CLARKE (2001) quoted a kid survival value of 70%, while the Parc National de la Vanoise (1983) quoted a value of 67%. In Northern French Alps, LOISON *et al.* (1994, in FORSYTH & CLARKE 2001) found a value of 58%. The χ^2 test detected a great variation over time: this doesn't surprise, as kid survival depends on several factors, such as the date of birth, kids' weight and the availability of maternal milk within the first 2 months of life (DEMATTEIS *et al.* 2001). These parameters are directly dependent on the climatic conditions, which, in Alpine environments such as the Alpe Colina study area, are highly variable throughout the years: there is no such a thing as a 'typical' juvenile survival for ungulates, it is extremely variable from year to year (see GAILLARD *et al.* 2000).

ANNUAL INCREASE

The observed mean annual increase was 5.7%. CAPURRO *et al.* (1997) showed that, for a chamois population of the Italian Alps, natural mortality and hunting results were additive. In the light of this, the percentages of both annual increase (5.7%) and hunted animals (7.4%) might be summed and, thus, a hypothetical annual increase equal to 13.1% might be obtained. Such a value is actually aligned to values commonly accepted to be found in natural conditions, between 10 and 20% (PFLIEGER 1982; Weber 2001; CORTI 2002; TOSI *et al.* 2003) though, theoretically, it might reach 25% (CORTI 2002). However, the discussion regarding additive vs. compensatory mortality is still open and further studies are required to clarify this aspect. Nevertheless, since the study population inhabited mainly a protected area and small percentage of chamois were yearly hunted, natural mortality and hunting might plausibly be considered additive. On the other hand, the 13.1% value still appears fairly low, if compared to that quoted by Weber (2001), 38% for a colonizing population on the

Sancy massif (France), or by PEDROTTI (1989), 30% for a population on the Orobic Alps and PAGANIN & MENEGUZ (1997), 25% for an Italian reintroduced population. The χ^2 test detected significant changes over time, likely due to both overestimations quoted before and poaching actions.

DENSITY

Leaving aside years 1995 and 1996, when densities were likely overestimated, afterwards, the population density didn't show large variations over time, and settled around 6 chamois/100 ha. It is well-known density can vary according to the environmental features and the management of both environments and populations (PEDROTTI & TOSI 2001). The observed value appears rather low, if compared to those quoted in the existing literature: 11-20 chamois/km² within suitable environments (TOSI *et al.* 2003), 8-10 individuals within environments at mean altitude with mean snow-cover (Weber 2001). The observed value is even lower if compared to those quoted, in France, by Weber (2001) and PFLIEGER (1982), 20-30 chamois/100 ha or, in Italy, by MUSTONI *et al.* (2002), 40 chamois/100 ha within the Alpi Marittime Natural Parc. Greatest values are usually reached within protected areas: since the study population inhabits, mainly, a protected area, its density might be considered fairly low indeed; most likely, the factors limiting the density might be identified in hunting and poaching, which can really lower its value: POUBELLE *et al.* (1989) observed that, actually, within a hunting area the density level lowered to the half of the value registered within a close protected area. Densities over the period 1993-2004 showed faint variations and, most of all, rather low values which, likely, couldn't trigger any density dependence in the demographic parameters above.

HUNTING MANAGEMENT

From 1993 to 2000, a greater number of male chamois were hunted, on the whole, even though a greater presence of females was assessed. It is right to point out, however, that the Alpine chamois is characterized by scarce sexual dimorphism, thus some misidentifications might have occurred in hunting. Nevertheless, preference in hunting males, by hunters or poachers, might be assumed, as already pointed out by GINSBERG & MILNER-GULLAND (1994). This greater hunting incisiveness toward males evidently resulted into a lower presence of this class: consequently, from 2001 a greater number of females were yearly hunted. On the whole, a greater number of females were hunted so far: therefore, the hunting management can't give explanation for the biased sex ratio toward females detected in 2004. This gives evidence for other factors limiting the male presence: among them, as already pointed out above, mainly natural mortality and poaching. Observing the mean age of hunted adults, it emerged that male mean age (5.6 years) is significantly lower than female's (9.3 years), as confirmed by the z-test. This might give evidence for a greater hunting incisiveness toward males, though even in an unhunted population one would expect males to be on average younger than females, because of their higher natural mortal-

ity. Rather than legal hunting, poaching might concur to give explanation for such a situation. In any case, it is unlikely to be explained by emigration: as a matter of fact, if emigration played a key role, likely younger individuals would emigrate, not older ones and, thus, there would have been, presumably, mean age increases.

Conclusion

This research allowed us to obtain deeper knowledge of a chamois population so far scarcely studied. There emerged a population with a numerical rising trend, in contrast with low values of annual increase which might have been limited by poaching actions. Poaching might also explain the heavily biased sex ratio in favour of females, which, on the other hand, could partially be justified by natural mortality. Further studies are required to investigate the respective roles of such limiting factors, as well as to clarify the density dependence or independence of specific and generic birth rates, which, anyhow, presented mean and high values, respectively (this might give evidence for a good reproductive success). In the present form, harvesting regime, due to both legal hunting and poaching, might bias sex ratios and lower demographic values, even though, compared to other hunted populations, the parameters of the study population appear being more balanced, which might be proof of the important role played by the protected core area in mitigating the harvesting effects.

REFERENCES

Allaine J., Houssine H., Gaillard J. M., 1990 - *Etude de la variabilite spatio-temporelle d'un indice de reproduction dans une population de chamois* (Rupicapra rupicapra). Gibier Faune Sauvage, 7: 85-94. (In French)

Apollonio M., 2004 - *Gli ungulati in Italia:* status*, gestione e ricerca scientifica.* Hystrix Italian Journal of Mammology, 15 (1): 21-34. (In Italian)

Bonenfant C., Gaillard J. M., Klein F., Hamann J. L., 2005 - *Can we use the young:female ratio to infer ungulate population dynamics? An empirical test using red deer* Cervus elaphus *as a model.* Journal of Applied Ecology, 42: 361-370.

Bubenik A.B. & Schwab P., 1975 - *Structure des populations de Chamois. La simulation et sa signification pour la regulation des effectifs.* Bull. Office National de la Chasse, spec. Etud. Sci. Tech., 1975 (3): 195-198. (In French)

Capurro A.F., Gatto M., Tosi G., 1997 - *Delayed and inverse density dependence in a chamois population of the Italian Alps.* Ecography, 20: 37-47.

Casanova P., Capaccioli A., Cellini L., 1993 - *Appunti di Zoologia Venatoria e Gestione della Selvaggina.* Ed. Polistampa, Firenze. (In Italian)

Clutton-Brock T.H., 1991 - *Sport and wise use of ungulate populations.* Gibier Faune Sauvage, 8: 309-317.

Corti R., 2002 - *Le chamois et l'isard.* Paris: Office National Chasse Faune Sauvage, (broch. n. 18), 36 pp. (In French)

Credaro V. & Pirola A., 1975. *La vegetazione della Provincia di Sondrio.* Amministrazione Provinciale di Sondrio e Banca Piccolo Credito Valtellinese, Sondrio, 104 pp.

Dematteis A., Tizzani P., Meneguz P.G., 2001 - *Il camoscio alpino: dinamica di popolazione.* In Lovari S. (ed.) Il camoscio, Habitat, 114: 36-44. (In Italian)

Festa-Bianchet M., 2003 - *Exploitative wildlife management as a selective pressure for life-history evolution of large mammals.* In: Apollonio M, Festa-Bianchet M., Animal behaviour and wildlife conservation, Island Press, Washington D.C., 322 pp.

Forsyth D.M., Clarke C.M.H., 2001 - *Advances in New Zealand mammology 1990-2000: Chamois.* Journal of The Royal Society of New Zealand, 31 (1): 243-249.

Gaillard J.-M., 1993 - *Analyse des recensements de chamois realises de 1984 a 1992 dans le Parc National des Ecrins.* Villeurbanne, Univ. Lyon I-CNRS, 22 pp. (In French)

Gaillard J.-M., Festa-Bianchet M., Yoccoz N.G., 1998 - *Population dynamics of large herbivores: variable recruitment with constant adult survival.* Trends in Ecology and Evolution, 13: 58-63.

Gaillard J.-M., Festa-Bianchet M., Yoccoz N.G., Loison A., Toigo C., 2000 - *Temporal variation in fitness components and population dynamics of large herbivores.* Annual Review of Ecology and Systematic, 31: 367-373.

Garin J., Herrero J., 1997 - *Distribution, abundance and demographic parameter of the Pyrenean Chamois (Rupicapra p. pyrenaica) in Navarre, Western Pyrenees.* Mammalia, 61 (1): 55-63.

Ginsberg J.R., Milner-Gulland E.J., 1994 - *Sex-biased Harvesting and Population Dynamics: Implication for Conservation and Sustainable Use.* Conservation Biology, 8 (1): 157-166.

Gonzalez G., Crampe J.-P., 2001 - *Mortality patterns in a protected population of isards* (Rupicapra pyrenaica). Canadian Journal of Zoology, 79: 2072-2079.

Houssin H., Loison A., Jullien J.M., Gaillard J.M., 1994 - Validite de la methode du pointage-flash pour l'estimation des effectifs de chamois (*Rupicapra rupicapra*). Gibier Faune Sauvage Game Wildl., 11: 287-298. (In French)

Langvatn R., Loison A., 1999 - *Consequences of harvesting on age structure, sex ratio and population dynamics of red deer* Cervus elaphus *in central Norway.* Wildlife Biology, 5 (4): 213-221.

Levet M., Apollinaire J., Catusse M., Thion N., 1995 - *Elements demographiques, comportement spatial et dispersion d'une population d'Isard* (Rupicapra p. pyrenaica) *en phase de colonisation.* Mammalia, 59 (4): 489-500. (In French)

Loison A., Toigo C., Apollinaire J., Michallet J., 2002 - *Demographic processes in colonizing populations of isard* (Rupicapra pyrenaica) *and ibex* (Capra ibex). J. Zool. Lond., 256: 199-205.

Mustoni A., Pedrotti L., Zanon E., Tosi G., 2002 - *Gli ungulati delle Alpi: biologia, riconoscimento e gestione.* Nitida Immagine Editrice, Cles, Trento, 538 pp. (In Italian)

Paganin M., Meneguz P.G., 1997 - *La reintroduzione del Camoscio alpino* (Rupicapra rupicapra) *sull'Altopiano di Asiago: primi risultati.* In: III Convegno nazionale dei biologi della selvaggina, Bologne 9-11 fevrier 1995, Spagnesi M., Toso S., Genovesi P. eds., Ricerche Biologia della Selvaggina (suppl.), 27: 679-683. (In Italian)

Parc National De La Vanoise, 1983 - *Dynamique et comportement de populations De Chamois En Vanoise.* Parc National De La Vanoise, 24 pp. (In French)

Pedrotti L., 1989 - *Struttura della popolazione di camoscio* (Rupicapra rupicapra rupicapra) *delle Alpi Orobie.* Tesi di Laurea in Scienze Biologiche, Università degli Studi di Milano, Anno Acca-

demico 1988-89. (In Italian)

PEDROTTI L., TOSI G., 2001 - *Camoscio delle Alpi*. In Prigioni *et al.*, Atlante dei Mammiferi della Lombardia. Assessorato all'Agricoltura, Regione Lombardia, 325 pp. (In Italian)

PFLIEGER R., 1982 - *Le Chamois, son identification et sa vie. Collection "grand gibier"*. Éditions Gerfaut Club, Paris. (In French)

PFLIEGER R., BAUER J.J., 1986 - *Bilan de 10 annees de chasse du chamois vosgien*. Chasse Alsace Lorraine 9: 5-11 (1ere partie). (In French)

POUBELLE F., PERRIER J., BANTIN L., MARTINET O., 1989 - *Etude demographique de deux populations de chamois* (Rupicapra rupicapra) *dans le massif de la Vanoise (Savoie-France). Comparaison entre une population situee en zone de chassee et une population situee en zone protegee*. In: Gamswildsymp.-Symp. Chamois, Ljubljana, 25/26.X.1988, Paris-Munich, C.I.C.: 395-424. (In French)

ROSÁ R., RIZZOLI A., PUGLIESE A., GENCHI C., CITTERIO C., 1997 - *Models for macroparasitic infections of chamois* (Rupicapra rupicapra *L.) in the Brenta mountain group (Trentino, Italy)*. Report N. 12, Centro di Ecologia Alpina, Sardagna (TN).

SOLBERG E.J., SAETHER B.-E., STRAND O., LOISON A., 1998 - *Population dynamics of a harvested moose* (Alces alces*) population in a variable environment*. Journal of Animal Ecology, 68: 186-204.

SOLIANI L., 2004 - *Manuale di statistica per la ricerca e la professione*. Available at: http://www.dsa.unipr.it/soliani/soliani.html (In Italian)

STRINGHAM S.F., BUBENIK A.B., 1975 - *Condition physique et taux de survie du chamois* (Rupicapra rupicapra *L.) en function des classes d'age et de sexe de la population*. Bull. Office National de la Chasse, 3: 199-224. (In French)

TOÏGO C. & GAILLARD J.-M., 2003 - *Cause of sex-biased adult survival in ungulates: sexual size dimorphism, mating tactics or environmental harshness?*. Oikos, 101 (2): 376-384.

TOSI G., PEDROTTI L., MONACO A., SCHERINI G.C., 1996 - *Progetto camoscio Monte Baldo*. Settore tutela faunistico ambientale, Provincia di Verona, 297 pp. (In Italian)

TOSI G., MARTINOLI A., PREATONI D., CERABOLINI B., VIGORITA V., 2003 - *Foreste e biodiversità faunistica in Lombardia*. Assessorato all'Agricoltura, Regione Lombardia, 563 pp. (In Italian)

WEBER E., 2001 - *Le Chamois et l'Isard (identification, moeurs, sexualité, maladies, réintroduction…)*. Ed. Delachaux et Niestlé, Lausanne, 192 pp. (In French)

Lavoro pervenuto il 20.11.07, accettato il 30.04.08