Allegato 2b_2

Dynamics of two ungulate populations in a mountain habitat: density dependence and climatic effects

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Introduction

Long-term climatic changes are indubitably affecting living systems (Parmesan & Yohe 2003) and their effects are expected to be particularly evident in extreme environments, i.e. at higher latitudes and altitudes (Root et al. 2003). Mountain areas, with their striking variety of climatic, vegetation and hydrological conditions occurring over relatively short horizontal distances (Whiteman 2000), indeed offer a unique opportunity to investigate the possible impacts of climate change on their biotic components (Beniston 2003). Disentangling and forecasting the potential effects of environmental changes on the life history traits and growth of animal populations living in mountainous areas (Coulson et al. 2001, Ozgul et al. 2010) has thus become a major endeavour for ecologists and conservationists.

Recent research on population dynamics, however, has emphasised the need to allow for the interactions between extrinsic factors –e.g. climate– and other sources of variation such as density-dependent food limitation and demographic structure, to better comprehend the mechanisms underlying wildlife numerical fluctuations (Gaillard et al. 2000, Coulson et al. 2001). To this end, mountain ungulates represent an appealing *taxon*, given their different age- and sex-dependent allocation of resources at different times of the year, and the predictable –yet highly variable– seasonality of their habitats.

Although there is a general consensus about the importance of the interaction between density and winter conditions in shaping the growth rate of mountain ungulate populations (Jacobson et al. 2004, Mignatti et al. 2012, Willisch et al. 2013), the impact of sex- and age-related physiological and behavioural mechanisms still remains to be fully clarified. For example, following great reproductive costs during the rutting season, adult males of polygynous species are expected to be more vulnerable than females to unfavourable environmental conditions (Toïgo and Gaillard 2003, Mysterud et al. 2004). Although Willisch et al. (2013) found that adult male chamois *Rupicapra rupicapra* are more affected by winter conditions than adult females, Jacobson et al. (2004) found a weak relationship between population size and adult *sex-ratio* in the Alpine ibex *Capra ibex*. Furthermore, although between-year variation in ungulate population growth is generally thought to be mainly affected by winter juvenile survival (Gaillard et al. 2000), through a combination of density-dependent processes and extrinsic factors such as starvation in snowy winters (Loison & Langvatn 1998), Jacobson et al. (2004) suggest winter adult survival as the main driver accounting for the numerical fluctuations of a protected population of Alpine ibex. Several other extrinsic factors, however, may have major impacts on the population dynamics of mountain ungulates: among the others, the state of pastures (Garel et al. 2011), parasite infections (Pioz et al. 2008) and interspecific competition (Forsyth & Hickling 1998).

Taking advantage of the availability of long-term series of count data, our first aim was to investigate the effects exerted by intrinsic and extrinsic factors on the demographic parameters of the protected populations of Alpine chamois in the Gran Paradiso National Park (Italy) and of the red deer *Cervus elaphus* in the Swiss National Park (Switzerland). The chamois, a nearly-monomorphic mountain-dwelling ungulate excellently adapted to live in rugged and rocky terrains, is the most abundant mountain ungulate of Europe and the Near East (Corlatti et al. 2011). Although the chamois, as a Genus, is not threatened (*sensu* IUCN), some populations of the Alpine subspecies in Europe lately showed a decreasing trend and other *Rupicapra* subspecies are threatened (Corlatti et al. 2011). Red deer is a large grazer with a holarctic distribution. Its adaptability allows the colonization of a wide range of habitats, from sea level to high mountains. Despite a general decreasing trend in Europe in historical times due to direct persecution and removal of suitable habitat, during the last decades this species underwent an increase of both populations abundance and area of occurrence throughout Europe.

In accordance with other studies, we expect that greater snow depth during winter should strongly affect the growth rate of chamois population, through a negative impact on demographic parameters such as survival and fecundity (Jonas et al. 2008, Gonzalez & Crampe 2001, Willisch et al. 2013).

The dynamics of red deer mountain populations is poorly known, however we expect winter weather to affect mainly winter calf survival, as it happens in the northernmost part of the red deer range (Loison & Langvatn 1998).

Because extreme age-classes are expected to be particularly sensitive to unfavourable environmental conditions (Solberg et al. 2001), we predict that kid/calf winter survival should represent one of the main drivers of the two ungulates numerical fluctuations. Milder spring-summer weather conditions, possibly through to a shift in plant phenology and the consequent reduction of body mass, may as well cause a reduction of survival and fecundity rates (Loison & Langvatn 1998, Rughetti & Festa-Bianchet 2012). Given the potential for resource competition between Alpine chamois and ibex (Trutmann 2009) and between red deer and chamois (Homolka & Heroldova 2001) we also investigate the potential impact of ibex density on the inter-annual variation of chamois abundance and of chamois density on red deer density.

Population models can also help investigating how intrinsic and extrinsic factors may influence not only the past, but also the future dynamics of wildlife populations (Forchhammer et al. 1998). Our second aim was therefore to predict the response of chamois population to expected climate change, by projecting the dynamics of the studied population under the climatic conditions predicted by a regional climate model.

Methods

Meteorological data

Daily temperature (minimum and maximum), precipitation, and snow depth were collected in the Gran Paradiso National Park (hereafter GPNP) by the Serrù station, at an elevation of 2240 m, available from 1962, and in the Swiss National Park (hereafter SNP) by the Buffalora station, at an elevation of 1970 m, operating from 1960 but with snow depth data available only until 1998.

For subsequent analyses, the daily mean temperature (as the average between minimum and maximum temperature), and the total number of days with continuous snow cover in each winter were computed. Then the mean, minimum and maximum temperature, precipitation, and snow depth were averaged across different critical season in the life cycle of the species. For chamois the selected seasons were: 1. early winter (November-December), 2. whole winter (November-May, as in Jacobson et al. 2004), 3. spring (May-June, corresponding to the birth season), 4. spring-summer (April-July, as in Rughetti & Festa-Bianchet 2012). For red deer the selected seasons were: 1. autumn (September-October, corresponding to the rut period), 2. early winter (November-

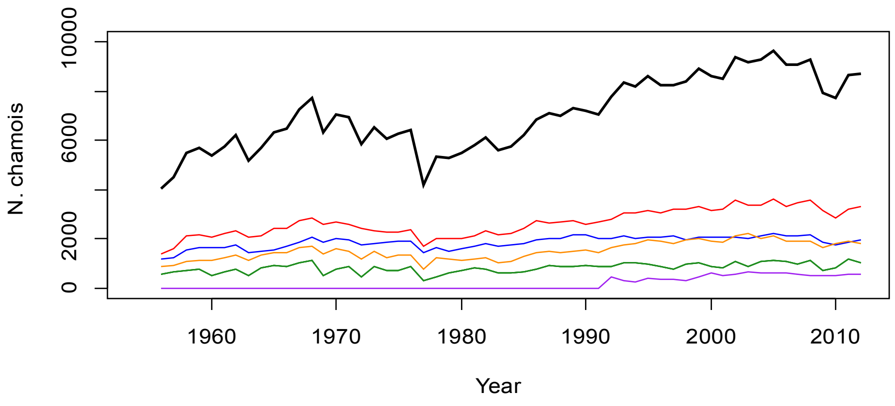
December), 3. whole winter (November-March), 4. spring (May-June, corresponding to the birth season), 5. spring-summer (April-July).

For spring and spring-summer seasons we considered both the variables at time *t+1* (between the two counts that form the growth rate) and at time *t* (before the first of the two counts that form the growth rate, see below).

Count data

In the GPNP, each autumn about 30 Park rangers conduct a ground count of the chamois and ibex populations by walking over established routes within assigned surveillance zones, which have an average area of about 10 km^2. Wardens classify the observed individuals as kids, yearlings, adult males, adult females or indeterminate adults. The census of the entire park is conducted over two consecutive days in September, and data are available from 1956 to 2012 (Fig. 1).

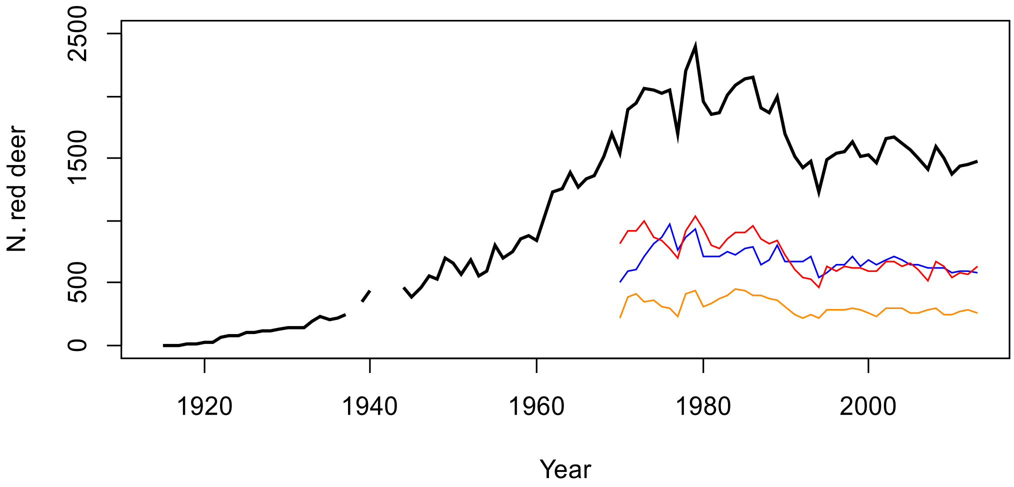
Fig. 1. Number of total chamois (bold line) and of different age/sex classes (blue: adult males, red: adult females, purple: indeterminate adults, green: yearlings, orange: kids) from1956 to 2012 in GPNP.



Until 1999 wardens carried out also a chamois count in spring. Correlation between the two yearly counts is rather high (adults: r=0.91; yearlings: r=0.90; kids: r=0.93), but the ratio between sighted and actually present animals is small (average of sighted marked animals in 2000-2001: 20%) and the yearly observation error is unknown.

In the PNS, red deer had been eradicated in the middle of the 19th and they reappeared 50 years later, migrating from northern and central Graubünden. Red deer were counted in the Park from 1918, when the first individuals were sighted, however only from 1970 they were classified as calves, adult females and adult males (yearlings were included in the age class of adults). Therefore we used data from 1970 to 2013 for the analyses, when the population had already reached an equilibrium (Fig. 2). Data on chamois population of the PNS were available for the same time period.

Fig. 2. Number of total red deer (bold line) and of different age/sex classes (blue: adult/yearling males, red: adult/yearling females, orange: calves) from1918 to 2013 in SNP.



Chamois indeterminate adults were distributed each year among the male and female adults age classes in the same proportion as the one observed between determinate males and female adults. From chamois count data, the following demographic parameters were computed:

1. population growth rate

were N_t is the total number of counted chamois at time t;

$$R_t = log \frac{N_{t+1}}{N_t}$$

2. adult survival (which include also yearling survival)

were M_t, F_t, and Y_t are the number of adult males, adult females and yearlings counted at time t;

$$S\_ad_t = \frac{M_{t+1} + F_{t+1}}{M_t + F_t + Y_t}$$

3. kid survival

$$S\_k_t = \frac{Y_{t+1}}{K_t}$$

were K_t, is the number of kids counted at time t;

4. weaning success

$$W_t = \frac{K_{t+1}}{F_{t+1}}$$

which, in this form, include both fecundity of females and kids survival during their first months of life.

From red deer count data, the following demographic parameters were computed:

1. population growth rate

$$R_t = log\frac{N_{t+1}}{N_t}$$

were N_t is the total number of counted deer at time t;

2. survival (which include both calf and yearling/adult survival)

$$S_t = \frac{M_{t+1} + F_{t+1}}{M_t + F_t + C_t}$$

were M_t, F_t, and C_t are the number of adult/yearling males, adult/yearling females and calves counted at time t;

3. male survival

(assuming a balanced sex-ratio at birth)

$$S\_m_t = \frac{M_{t+1}}{M_t + \frac{1}{2}C_t}$$

4. female survival

$$S\_f_t = \frac{F_{t+1}}{F_t + \frac{1}{2}C_t}$$

5. weaning success

$$W_t = \frac{C_{t+1}}{F_{t+1}}$$

which, again, include both fecundity of females (unfortunately, also yearling – non-breeding females are included in the computation) and kids survival during their first months of life.

Data filtering

Since density estimates were potentially affected by observation errors, a state-space model (SSM) was used to filter the original raw data and disentangle sampling error from environmental variability. This was necessary to avoid biases in the detection of a negative relationship between population growth rate and population size (Freckleton et al. 2006, Lebreton & Gimenez 2013).

SSMs, when used for analyzing time series of population abundances, allow the joint estimation of the likelihood of the amount of observation error along with the amount of process noise. In particular, we adopted a linear SSM with a Kalman filter approach assuming a Gompertz density dependence, which represents environmental stochasticity as a lognormal stochastic process and includes lognormal observation errors (Dennis et al 2006). For parameter estimation, we used the PROC MIXED of SAS 9.2 (SAS Institute Inc., Cary, NC) following the procedure step by step described in the Appendix B of the paper by Dennis et al. (2006).

Demographic parameters were then computed again from filtered data.

Analysis methods

The effect of density dependence (expressed as logN_t, following the Gompertz population model, or the number of adults at time *t*, or the number of male or female adults at time *t*) and climatic indexes on filtered series of population growth rate and demographic parameters of the Alpine chamois in GPNP and red deer in PNS was investigated through a series of Generalised Linear Models. All linear combination of variables (and first-order interactions between density and climatic variables) were tested. Models containing two variables that were significantly crosscorrelated were discarded in order to reduce problems with parameter estimations (Zuur et al. 2007). Best-performing models were selected through Akaike Information Criterion. (Burnham & Anderson 2002).

Population projections

To estimate future population trends, we forced the best-performing models with the time series of meteorological variables (temperature, precipitation, and snow depth) generated by the PROTHEUS regional climate model (Artale et al. 2010, Dell'Aquila et al. 2011) for the A1B scenario in the period 2013-2050. PROTHEUS is a state-of-the-art coupled ocean-atmosphere regional climate model developed by ENEA and ICTP for the Mediterranean region based on the RegCM3 atmospheric model and the MITgcm ocean model. The model configuration has a uniform grid spacing of 30 km; for the present study, we used the output of the model for the grid cell including the largest proportion of GPNP area.

Snow depth is provided in mm of snow water equivalent; for simplicity we assumed a constant snow density within the year and throughout the simulation period. To standardize the model's meteorological variables for subsequent analyses, all PROTHEUS time series were scaled to have the mean and variance of the observed Serrù series in the period 1962-2012.

First, a population projection was performed using the selected model for population growth rate. Then a projection for each demographic parameter was carried out. If density dependence was present in demographic parameters GLMs, a constant density (corresponding to the average density for the period 2013-2050 obtained with the projection of population growth rate) was considered in the simulations, in order to highlight the effect of a changing climate. Finally, a population projection was performed using the results of all the demographic parameters empirical models.

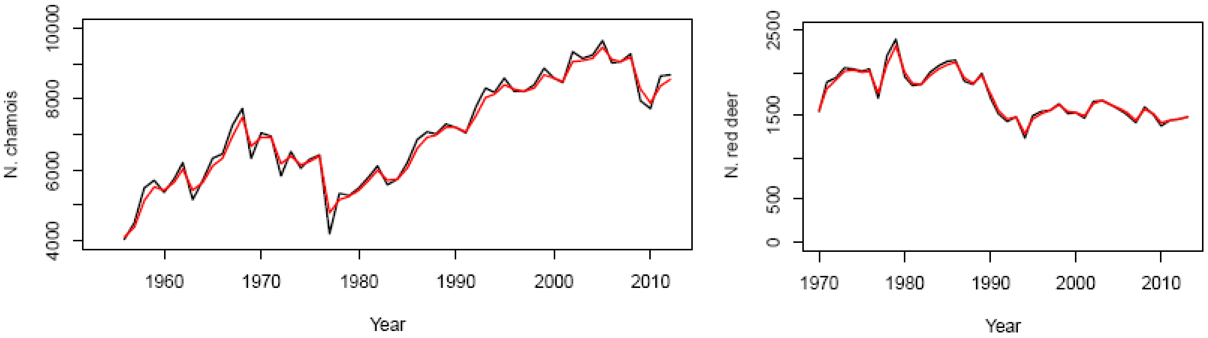
For each projection, 1000 runs were performed to account for uncertainty in empirical models.

Results and discussion

Over the study period, chamois population showed a significant increasing trend (R^2=0.69, p<0.0001, +73.04±6.62 chamois per year) (Fig.1). For the naturally colonizing population of red deer in SNP, there was a steady increase during the recovering period (1918-1979: R^2=0.89, p<0.0001, +35.72±1.64 deer per year); after the irruption, the population started to decrease (1980-2013: R^2=0.52, p<0.0001, –17.43±2.94 deer per year) (Fig. 2).

The state-space model yielded series of population abundance that were filtered by measurement errors (Fig. 3).

Fig. 3. State-space model outputs for Alpine chamois in GPNP (left) and red deer in SNP (right). Black line: original series of abundance data; red line: filtered series



Weaning success, being a ratio between two measures taken during the same year, is not affected by the use of state-space model (Fig. 4 and 5). Time series of the other demographic parameters, on the other hand, are "polished" by excessive fluctuations due to sampling error. It is important to note that in the filtered series disappeared the unrealistic survival values over 1 (except for female red deer in SNP) (Fig. 4 and 5).

Figure 4. Population growth rate and other demographic parameters of Alpine chamois in GPNP computed from original (black line) and filtered (red line) series of abundance data.

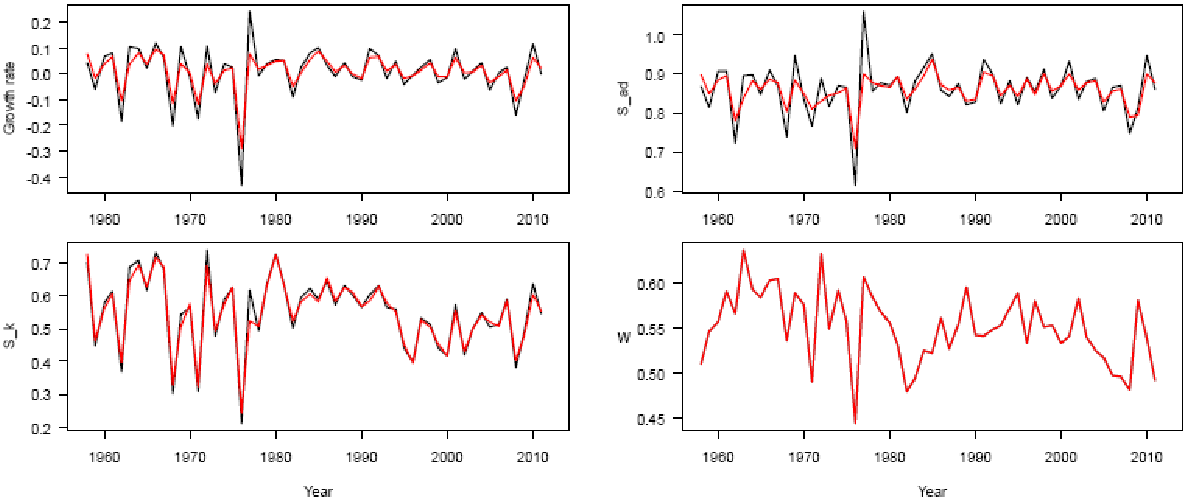
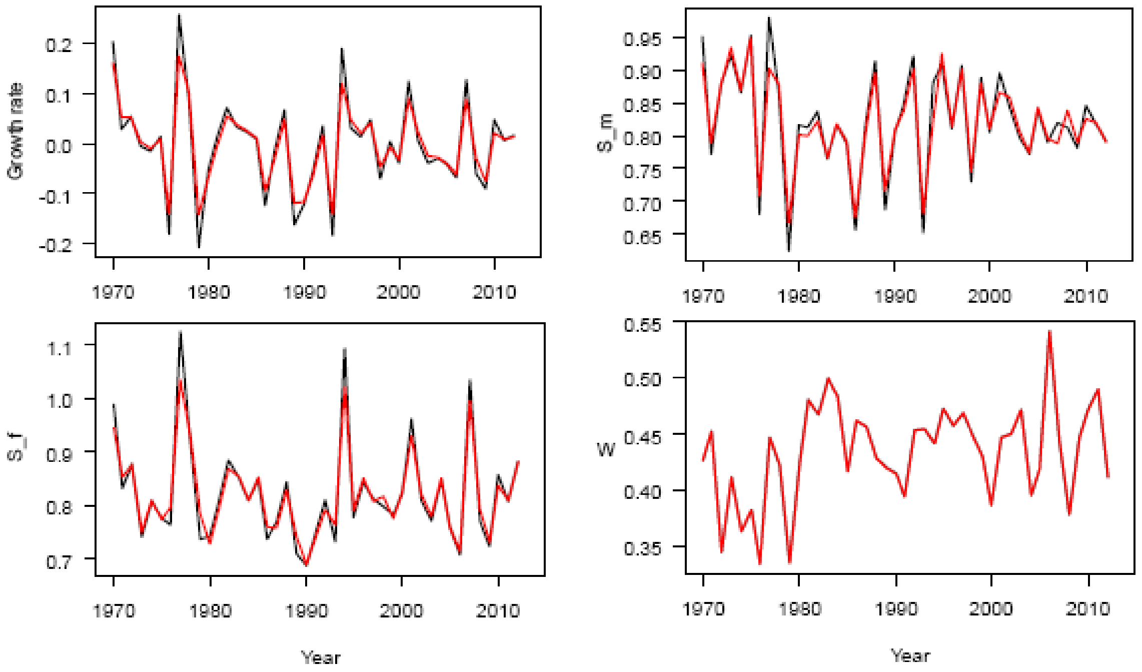


Fig. 5. Population growth rate and other demographic parameters of red deer in SNP computed from original (black line) and filtered (red line) series of abundance data.



Factors affecting demographic parameters of chamois

Results of selected models for population growth rate and other demographic parameters of Alpine chamois in PNGP are shown in Tab. 1.

Table 1. Selected GLMs for demographic parameters of Alpine chamois in PNGP. Significant effects are in bold.

Dependent variable	Intercept	$\log N_t$	$\log N_t$*S (winter)$_t$	Tmin(spring -summer)$_t$	S(spring-summer)$_t$	P(winter)$_t$	P(spring-summer)$_{t+1}$	P(spring)$_{t+1}$	R^2
R_t	**1.69±0.33**	**-0.18±0.04**	**-9.30×10^{-5} $\pm1.27\times10^{-5}$**				**-1.15×10^{-2} $\pm0.47\times10^{-2}$**		0.59
S_ad_t	**1.51±0.24**	**-0.07±0.03**	**-4.51×10^{-5} $\pm0.93\times10^{-5}$**						0.34
S_k_t	1.49±0.78	-0.09±0.08		**-1.36×10^{-2} $\pm0.69\times10^{-2}$**		**-3.84×10^{-2} $\pm0.74\times10^{-2}$**			0.46
W_t	**0.58±0.01**				**3.72×10^{-4} $\pm0.93\times10^{-4}$**	**-1.12×10^{-2} $\pm0.29\times10^{-2}$**		-3.99×10^{-3} $\pm2.13\times10^{-3}$	0.52

A density-dependent effect, due to resource competition, was detected in both growth-rate and age-specific survival models (but not significant for kid survival), while it was less important for weaning success. This latter result is in contrast with Willisch et al. (2013), who found density dependence also for kid/female ratio, likely mediated by intra-female competition that could depress fecundity.

Growth rate was negatively affected also by average snow depth in winter and precipitation in spring-summer. Adult survival showed lower variability than the other demographic parameters, and was affected only by average winter snow depth. Deep snow can limit access to food resources, with a consequent deterioration of body conditions and an increase in mortality. A negative effect of winter snow depth on population growth rate has been already found for different mountain ungulate species (Alpine chamois: Willisch et al. 2013; Alpine ibex: Jacobson et al. 2004; mountain goats: White et al. 2011). As for Alpine ibex (Jacobson et al. 2004), the interaction between density dependence and winter snow depth significantly affect growth rate and adult survival, indicating an amplification of intra-specific competition during harsh winters.

Together with winter precipitation, also a delayed effect of spring-summer temperatures negatively affected kid survival. This result is in accordance with Rughetti & Festa-Bianchet (2012), who found both a direct and a delayed negative effect of high spring-summer temperatures on body mass of yearling chamois, possibly due to the shortening of the period available to feed on high-quality plants. However, the effects of spring-summer conditions on population dynamics of this mountain ungulate has never been investigated.

Kid-female ratio was negatively affected by winter and spring precipitations, but positively affected by snow depth in the spring of the previous year. The latter effect could have been mediated by the body conditions of mothers, possibly favoured by higher water availability for pastures.

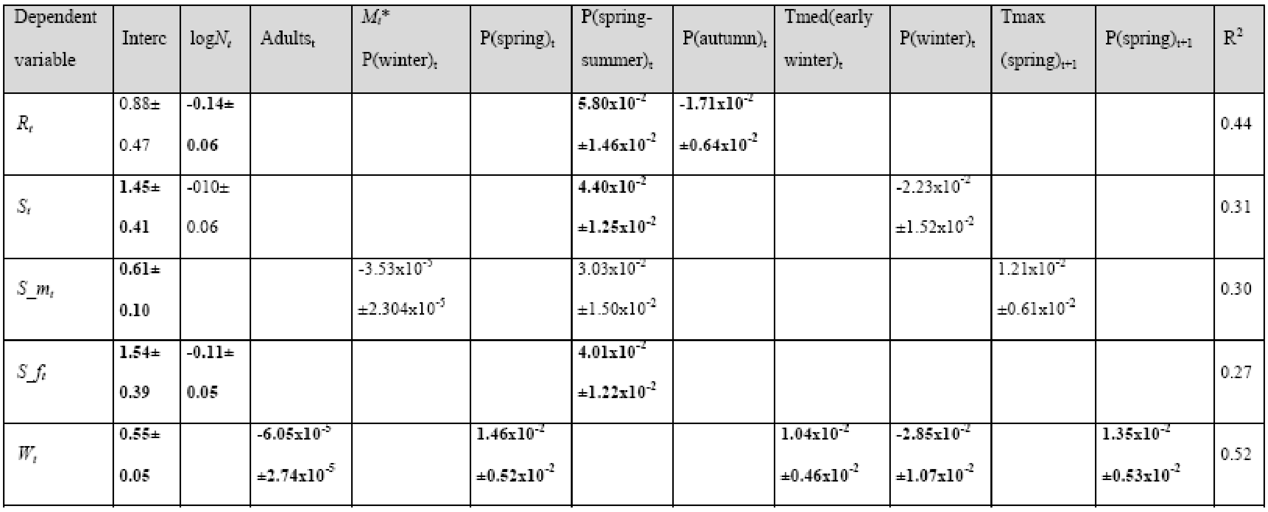
No effect of ibex density was detected in any of the demographic parameters.

In view of these results, on one hand climate change appeared to yield positive effects on the demography of Alpine chamois, through the shortening of the snow cover period which, in turn, allowed a higher survival of both juveniles and adults. Higher temperatures in spring/summer, however, had an opposite effect on fecundity and kids survival, possibly depressing population growth rate.

Factors affecting demographic parameters of red deer

Results of selected models for population growth rate and other demographic parameters of red deer in SNP are shown in Tab. 2.

Table 2. Selected GLMs for demographic parameters of red deer in SNP. Significant effects are in bold.



Dependent variable	Interc	logN_t	Adults$_t$	M_t* P(winter)$_t$	P(spring)$_t$	P(spring-summer)$_t$	P(autumn)$_t$	Tmed(early winter)$_t$	P(winter)$_t$	Tmax (spring)$_{t+1}$	P(spring)$_{t+1}$	R^2
R_t	0.88± 0.47	**-0.14± 0.06**				**5.80x10^{-2} ±1.46x10^{-2}**	**-1.71x10^{-2} ±0.64x10^{-2}**					0.44
S_t	**1.45± 0.41**	-010± 0.06				**4.40x10^{-2} ±1.25x10^{-2}**			-2.23x10^{-2} ±1.52x10^{-2}			0.31
S_m_t	**0.61± 0.10**			-3.53x10^{-5} ±2.304x10^{-5}		3.03x10^{-2} ±1.50x10^{-2}				1.21x10^{-2} ±0.61x10^{-2}		0.30
S_f_t	**1.54± 0.39**	**-0.11± 0.05**				**4.01x10^{-2} ±1.22x10^{-2}**						0.27
W_t	**0.55± 0.05**		**-6.05x10^{-5} ±2.74x10^{-5}**		**1.46x10^{-2} ±0.52x10^{-2}**			**1.04x10^{-2} ±0.46x10^{-2}**	**-2.85x10^{-2} ±1.07x10^{-2}**		**1.35x10^{-2} ±0.53x10^{-2}**	0.52

Density dependence was detected in all demographic parameters, however, while for population growth rate and female survival it is represented by a negative effect of population abundance, male survival it is negatively affected by male abundance and kid/female ratio by the number of adults/yearlings of the previous year. A negative effect of density on survival was already found in other red deer populations, mainly in calves (Coulson et al. 1997) and yearlings (Clutton-Brock et al. 1987), while for adult survival the results are contradictory (Gaillard et al. 1998, Albon et al. 2000). It is possible that the detection of density dependence in adult survival is function of population density that enhance resource competition, therefore our result could be justified by the high density during the study period.

While temperature in early winter affected only calf/female ratio (an effect already found in an extreme environment such as the northernmost part of the red deer range – Norway, Loison & Langvatn 1998 –, but not in Rhum, Coulson et al. 1997), autumn or winter precipitation negatively affected all demographic parameters, except female survival. At the beginning of winter, adult females are probably in better body condition than calves, juveniles and adult males (which loose 14–17% of their weight during rut, Mitchell et al. 1976), allowing them to cope with harsh winters. It is important to note that for both growth rate (R_t) and adult/calf survival (S_t) selected models included either autumn or winter precipitation (in both cases, competing models had ΔAIC=0.4), indicating that both periods are critical for this population. Winter conditions affect adult survival in high-density populations of red deer in Scotland (Albon & Clutton-Brock 1988), but not in a low-density population in Norway (Loison & Langvatn 1998). This indicates that winter harshness interact with intra-specific competition, explaining the interaction term in the male survival model in our study.

Spring temperature positively influenced male survival (a result already found by Loison & Langvatn 1998, and difficult to explain) while spring precipitation (during the birth season) positively affect calf/female ratio, likely by improving pasture quality for female during lactation and gestation. However, in the period where snow data are available (1970-1998), other important factors for weaning success are the negative effects of spring snow depth and the number of days with snow cover, indicating that extreme conditions are detrimental for fecundity and calf survival.

A delayed effect of spring or spring-summer precipitation positively affected all demographic parameters. Wetter conditions could in fact positively affect the quantity and quality of forage, and in turn body condition of both calves and adults, increasing both female fecundity (in particular that of young females, Imperio et al. 2012) and winter survival of all sex/age classes.

No effect of chamois density was detected in any of the demographic parameters of red deer in SNP.

Chamois response to climate change

The projection of chamois population in GPNP according to the PROTHEUS climate model and the results of empirical model for growth rate (Tab. 1) showed a significant decreasing trend (2013-2050: R^2=0.37, p<0.0001, -30.98±6.66 chamois per year) (Fig. 6a). However, the population is predicted to keep rather high numbers (average of the 50% quantile: 7816.65±93.09). The average abundance value obtained with this projection was then used as constant abundance value for the density dependence term of the projections of adult and kid survival.

The projection for adult survival (2013-2050: R^2=0.01, p=0.50) and weaning success (2013-2050: R^2=0.01, p=0.48) showed no trend, while kid survival showed a slightly decreasing trend (2013-2050: R2=0.08, p=0.04) (Fig 6b, d and c, respectively).

As a result, population projection performed using the results of empirical models of all demographic parameters showed a much stronger decreasing trend (2013-2050: R^2=0.89, p<0.0001, -90.86±5.20 chamois per year) (Fig. 7). The abundance predicted for the last forecasted decade (2040-2050: average of the 50% quantile: 5662.22±90.40) is comparable with the low numbers observed around 1960 and 1980. The age-structured population projection is therefore more pessimistic than the unstructured simulation. Mignatti et al. (2012) demonstrated that sex- and age-structured models have a better fit, hence are more realistic, than unstructured models. Ignoring climatic effects on the single demographic parameters could therefore lead to misleading results. In the case of Alpine chamois, global warming could be detrimental to population growth rate, by depressing kid survival. Future studies should aim addressing the effects of spring climate on pasture quality and, ideally, their effects on body mass and milk quality of pregnant and lactating females.

Fig. 6. Projections of population abundance and demographic parameters of chamois in GPNP for the period 2013-2050, according to the PROTHEUS climate model for the A1B scenario. Thick line: filtered time series of chamois abundance; thin line: 50% percentile, broken lines: 5–95% percentiles of the 1000 runs.

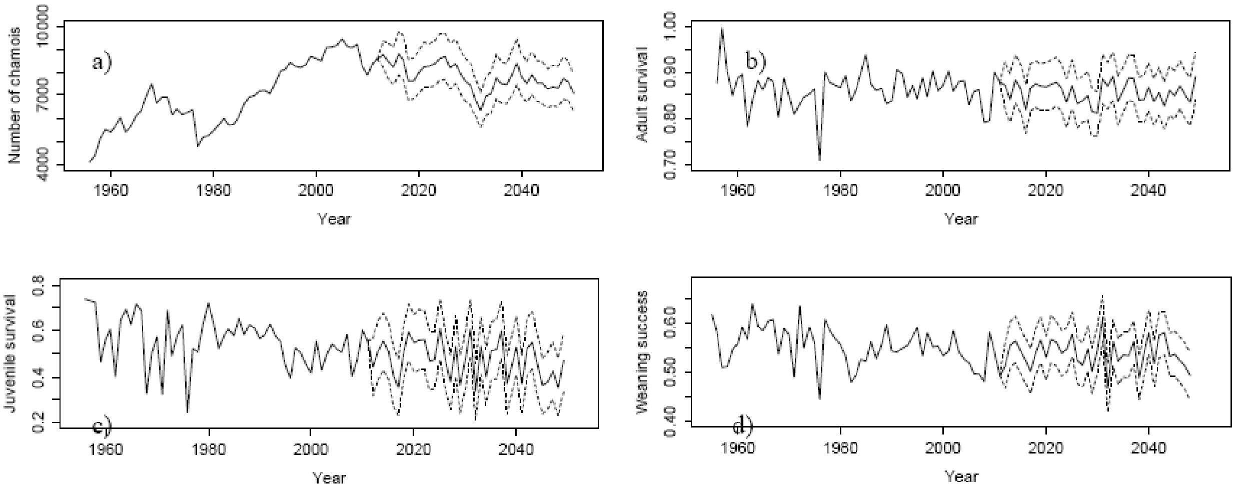
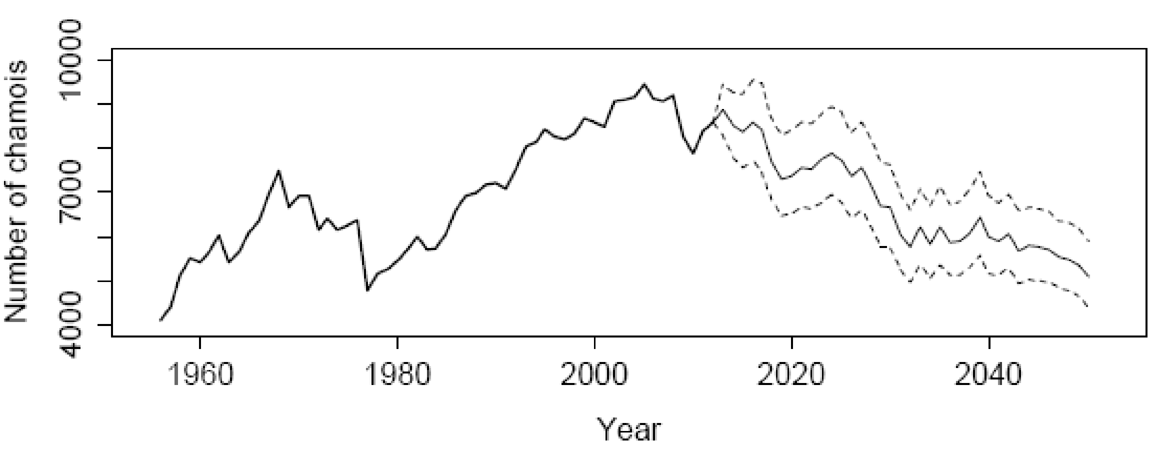


Fig. 7. Population projection of chamois in GPNP for the period 2013-2050, according to the PROTHEUS climate model for the A1B scenario and the empirical models for all demographic parameters. Thick line: filtered time series of chamois abundance; thin line: 50% percentile, broken lines: 5–95% percentiles of the 1000 runs.



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