Allegato 3b_4

Modelling the dynamics of a declining mountain ungulate population integrating total population counts and individual life history data

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Abstract

The Alpine ibex population in Gran Paradiso National Park (Northwestern Italian Alps) has suffered a dramatic decline over the last 20 years. Previous models, based on total count data, available since 1956, identified density dependence and winter snow cover as the main drivers of the population dynamics until it reached its peak in 1993, but were unable to predict the subsequent decline. The population fall-off is associated with a strong decline in kid survival which passed from an average of 0.58 (rate of kids which reach the yearling stage in 1981-1990) to an average of 0.35 in the last 10 years. Two main hypotheses have been proposed to explain this decline: 1) Ageing of the population: in ungulates older females are known to have lower fertility and produce less viable kids; 2) Mismatch between trophic and breeding phenology due to climate change. Here we use an integrated population modelling approach to explore the temporal variability in demographic parameters and modifications in the age structure in this population. We combine a state-space model of total population counts with capture-mark-resight, kid survival, and fecundity data collected over the last 25 years on individually tagged Alpine ibex. This approach permitted us to reconstruct age specific survival trajectories for years for which we have only count data available, get more accurate estimates of vital rates and contribute to disentangling the possible causes of the population decline.

Introduction

Long term population dynamics studies on free ranging large herbivores have a great importance both for wildlife management as for conservation due to the great role these species play in the ecosystems they inhabit (Gordon, Hester, and Festa-Bianchet 2004). Variation in demographic parameters (natality, juvenile survival, adult survival etc.) can have very different impacts on the dynamics of a population (Gaillard, Festa-Bianchet, and Yoccoz 1998). Temporal variability in demographic parameters of juvenile age classes (before the age of primiparity) appears to be responsible for most of the variability in the growth rate of wild ungulate populations (from 51% to 94%: Gaillard et al. 2000). Temporal modifications in these parameters due to exogenous factors, such as climate change, may therefore have a dramatic impact on the population dynamics of these species. For example in red deer (*Cervus elaphus*) in Norway, after increasingly warm winters, females gave birth to calfs that weighted less than calfs born after cold winters, probably because the earlier snowmelt in warm years causes an early onset and rapid progression of vegetation with the consequence of a shorter period of access to high quality forage (Post et al. 1997). Also in feral sheep (*Ovis aries*) juveniles were lighter at birth and had reduced survival after winters associated with an high North Atlantic Oscillation (NAO) index, while the same conditions improved survival of adults (Forchhammer et al. 2001). In Alpine ibex (*Capra ibex*), a decline in kid survival has been shown to be related with the progressive increase in the steepness of the rate of change of the normalized difference vegetation index (NDVI) (Pettorelli et al. 2007). Rapid changes in NDVI during the green-up period may reflect a shorter period of availability of high-quality forage, decreasing the opportunity for Alpine ibex to exploit high-quality forage. When the kids are born at the end of June, forage quality is already reduced and therefore births may not be synchronized any more with the peak in primary production of alpine pastures. Alpine ibex have been monitored for more than 50 years in the Gran Paradiso National Park (GPNP; North-western Italian Alps) providing a unique opportunity to analyze in detail the interplay between population dynamics and temporal variability in demographic parameters of a wild free-ranging large herbivore in the absence of hunting. In previous studies based on the census time series (von Hardenberg et al. 2000, Jacobson et al. 2004), we showed how the decline in average winter snow cover, recorded in the Alps starting from the mid eighties of the last century onwards, caused a strong increase in the population growth rate from 1985 to 1993 when the GPNP Alpine ibex population reached the record count of almost 5000 individuals. Subsequently, however, the population has seen a progressive and constant decline (53% from 1993 to 2009), with a historically minimum of 2321 Alpine ibex counted in September 2009. This is the lowest ibex count in GPNP since 1956, when ibex censuses started to be performed yearly on fixed dates and with a standardized protocol (Fig.1).

A predictive, out-of-sample model, built on the first 20 years of count data and based on the interaction between the effects of snow and density was able to predict the great population increase between 1985 and 1993 (Jacobson et al. 2004), but not the strong decline the population suffered afterwards. Besides our own past analyses, none of the other models explored so far on the GPNP Alpine ibex population time series (Lima and Berryman 2006) was able to represent simultaneously the population peak in the early nineties and the strong decline afterwards. The main limit of these previous population modeling exercises, with the exception of the attempt by Mignatti et al. (2012), is that they modeled the total counts only, ignoring the age structure of the population (Yoccoz and Gaillard 2006). Alpine ibex are long living, sexually dimorphic capital breeders characterized by overlapping generations, high adult survival and actuarial senescence (Toigo et al. 2007). Changes in the age structure of the Alpine ibex population, due to a decrease in the mortality rate of older individuals, with a resulting aging of the population could potentially have a strong impact on fecundity and survival of juvenile age classes, and thus, through the decline in recruitment, on the whole dynamics of the population (Yoccoz and Gaillard 2006). It is known that older female ungulates, due to reproductive senescence, besides having a reduced breeding output, on average have less synchronized birthing seasons, and can give birth to kids with reduced survival chances (Gaillard et al. 2000).

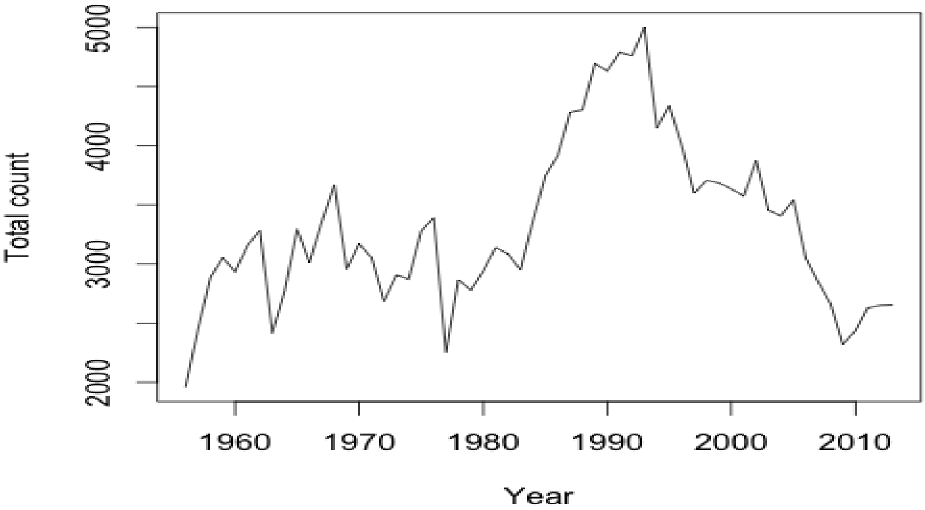

Fig 1. Total counts of Alpine ibex in Gran Paradiso National Park 1956-2013

In recent years there has been a surge in the development and application of integrated population modeling approaches (Besbeas, Freeman, and Morgan 2005) which, through the formation of a joint likelihood, integrate in the same model count data and individual based life history data. Besides providing more precise estimates of the population size and of the demographic parameters (Tavecchia et al. 2009), the integrated population models, gaining information from different sources of data, allow to estimate not directly measured "hidden" parameters (Besbeas and Freeman 2006). They therefore have the potential to reconstruct demographic parameters and temporal variations in the age structure for years in which these parameters have not been measured directly, but for which accurate sex and age specific count data is available, gaining information from independent individually based life history data available for part of the time series. Here we develop an integrated population model for the Alpine ibex in the Gran Paradiso National Park (GPNP), combining in the same analysis sex and age specific total counts available yearly since 1956 with individual based data (adult survival estimated from capture mark recapture and recovery data, yearly fecundity of individually tagged females, monthly kid survival estimated from capture mark recapture data for kids of recognizable mothers) available for the last 27 years. Our model incorporates actuarial senescence and reconstructs the variation in the proportional age structure of the population over time. Specifically, we use this statistical model to test for the hypotheses implied in the conceptual population model described hereafter.

A conceptual model of the Gran Paradiso Alpine ibex population dynamics

The population dynamics of Alpine ibex in GPNP from 1956 to nowadays can be divided in three phases: a first, stationary, cyclic phase lasting for about 20 years; a second, increasing phase in the following 10 years; and a third declining phase going on since 1993 (Fig 1). From 1956 to the beginning of the eighties of last century, the Alpine ibex population in GPNP has been cyclic with regular population crashes, associated with high density and extreme snow cover in the winter before (Jacobson et al. 2004). After that, winter snow cover started to decline, likely due to climate change, improving the winter survival of older individuals. As a consequence, the total population increased until reaching its maximum in 1993. The declining snow cover, as well as warmer winters cause anticipated snow melt in spring leading to an early onset of vegetation growth and a rapid green-up. This may result in a shorter period of access to highly digestible protein rich forage (Langvatn et al. 1996) possibly negatively affecting lactation and thus the growth of kids (Post et al. 1997) and ultimately reducing their survival probability. In a previous study on the same population (Pettorelli et al. 2007) we found a negative correlation between kid survival (estimated from count data only) and the rate of change in primary production in the green-up period (estimated from the normalized difference vegetation index (NDVI). The maximum changes in NDVI during the green-up appears to be related with a shorter period of availability of high-quality forage (Hamel et al. 2009).

Population density is as well known to strongly affect juvenile age classes in ungulates (Gaillard, Festa-Bianchet, and Yoccoz 1998) while adults appear to be mostly unaffected (Festa-Bianchet, Gaillard, and Côté 2003). Increasing population density may thus have additively accrued the mortality rate of kids. We hypothise that the effect of the declining survival of kids and thus of the consequent lack of recruitment on the dynamics of the total population was overshadowed, until 1993, by the effect of the increased longevity of a large proportion of adults (e.g. mortality rate of adults was lower than the recruitment rate). However, by 1993, the decline in the recruitment rate had reached the point of being lower than the mortality rate of adults and the population started to decline steadily, reaching its historic minimum in 2009. Besides the effects of increasing population density and of the shorter vegetation growing seasons, a second, possibly additive, demographic mechanism may explain the declining recruitment rate. As mentioned above, it is expected that the reduction in the mortality rate of adults should lead to an increse of the proportion of senescent females in the age structure of the population (N. Yoccoz and Gaillard 2006). It is known that older female ungulates, due to reproductive senescence, besides having a reduced breeding output, on average have less synchronized birthing seasons, and can give birth to kids with reduced survival chances (Bérubé, Festa-Bianchet, and Jorgenson 1999). Furthermore, the decline in recruitment will progressively reduce the proportion of prime-aged females, which in turn should lead to a decline in the average fecundity in the population. Therefore the decline in recruitment potentially amplifies its negative effects on the population in a positive feedback. Disentangling the relative contribution of density dependence, changes in the length of the vegetation growing season and changes in the age structure on recruitment and thus on the dynamics of the whole population is one of the objectives of the present work.

Methods

Study area and population

The Gran Paradiso National Park (GPNP) is a fully protected area established in 1922 in the North-western Italian Alps (45° 25'N, 7° 34'E) in part to protect the only surviving population of Alpine ibex. The park borders the Parc National de la Vanoise in France on the West and the Mont Avic Natural Park on the East. Alpine pastures, moraines, cliffs, glaciers and rock account for 59% of the 72,000 ha of the GPNP area. Alpine ibex use elevations ranging from about 800 m above sea level to beyond the upper limit of vegetation at about 3200 m. Alpine ibex has a protected status and is not hunted both in Italy as in France.

Although there have been a few sightings of lynx (*Lynx lynx*) and wolf (*Canis lupus*) has made a return to GPNP in the last years, large predators have been absent for most of the past 100 years. Research based on the analysis of wolf scats and the remains of predations, show that Alpine ibex are only marginally present in the diet of wolfs in GPNP, and predation is therefore believed to be a negligible factor in the dynamics of this ibex population (Palmegiani, Gazzola, and Apollonio 2013), as most ibex die of senescence, starvation or disease (Bassano, Durio, and Peracino 1992). The GPNP has been the source of ibex for many reintroductions in the Alps. Yearly removals for transplants never exceeded 1% of the park's ibex, and were of 0 - 0.5% in most years, and are thus assumed to have had a negligible impact on the population. The only other wild mountain ungulate in the park is the chamois (*Rupicapra rupicapra*).

Adult ibex are highly sexually dimorphic. Males weigh about 95-100 kg, about twice as much as females (Giacometti et al. 1997). Female ibex may produce their first kid at two years of age, although age of primiparity may be delayed in high- density populations, as in most other ungulates (Gaillard et al. 2000). Twins are almost never observed in the GPNP, but have been documented in captivity (Stüwe and Grodinsky 1987).

Count and individual life history data

Total counts of the GPNP Alpine ibex population have been conducted by park wardens on the first two days of September each year following the same standardized protocol since 1956. Each census has recorded the number of adult males (Nm), adult females (Nf), male and female yearlings (Ny), and male and female kids (Nk). 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. Ground counts of Alpine ibex have been shown to be a reliable index of changes in total population size (Largo et al. 2008). More details on the censuses in GPNP can be found in A. Jacobson et al. (2004). 446 adult Alpine ibex (358 males and 88 females), have been captured and individually tagged in the Gran Paradiso National Park since 1987. Field operators and wardens report all sighted individuals which are recorded as yearly Capture-Mark-Resight data. Most captures have been performed in the long term study area of Levionaz, where about 80% of males are currently tagged. Details on capture and tagging operations can be found in Brambilla et al. (2013). Fecundity and kid survival of individually tagged females are recorded yearly since 2000. Kids are considered having survived the winter if they are still observed together with their mothers the following june (i.e. they are recorded reaching the yearling stage). Metereological data, available since 1962 from a meteorological station at the Serru dam within the GPNP are provided by IRIDE spa. Details on the measurement of yearly average snow depth are provided in Jacobson et al. (2004). A measure of seasonal (from 1st July and 30th September) mean content of Crude Protein in pastures was estimated from NDVI data with methods explained in Ranghetti (2014). We tested also other estimates of phenology as described in Ranghetti (2014), which however are all highly auto-correlated. We therefore never fitted different estimates of phenology in the sam model.

Statistical methods

At the core of the integrated population model there is a state-space model for the yearly counts with the likelihood formed using the Kalman filter. The joint likelihood of the integrated population model was thus formed as the product of the following elements: Counts state-space model (likelihood formed using Kalman filter), Kid survival (binomial likelihood), Female productivity (binomial likelihood, assuming no twinning), Adult capture-mark-resight (CMR) data (age and time-dependent product multinomial likelihood). A diffuse initialisation was used based on first count observation. Covariates were fitted with a linear logistic link function. All covariates have been standardized. Capture and resight probability was modeled including with an additive effect for the increased capture and observation effort in the Levionaz study area compared to the rest of the Park (Levionaz effect). The effect of age of females on productivity was modeled with two linear regressions with a breakpoint at 8 years of age.

Survival senescence of adult females and males was separately modeled by a Gompertz curve with:

$$\phi_{(a,t)} = e^{-\rho e^{\sigma a}}$$

where:

a = age
t = time
ρ = logit(*) - * is a linear additive function of covariates
σ = logit(*) - * is a single parameter, which represents the rate of decline

Model selection was perfomed on the integrated population model using AIC. All models were implemented in MATLAB (The MathWorks, Inc.).

Results and discussion

The results of model selection are provided in table 1. The best fitting integrated model had the following structure (in parenthesis the sign of the effect for the covariates included in the final model after model selection):

Capture probability – time-dependent with additive Levionaz effect (positive)
Recovery probability – Levionaz effect (positive)
Adult survival probability – sex-dependence, age[1:4] constant, Gompertz curve (above age 5) to model senescence, snow depth (positive), interaction snow*population size (negative)
Kid survival probability – snow depth (negative), population size (negative), snow*population size (positive), Crude Protein content (positive)
Productivity – linear regression age[2:7] (positive), linear regression age [8+] (negative)
Observation error - constant

Table 1. Model Selection of alternative integrated population models for Alpine ibex population in the Gran Paradiso National Park.

Model	k	(-log L)	AIC	Delta AIC
*p(time+leviona),lambda(leviona),phi(sex*Gompertz+sex*[snow+snow*pop size])phi_kid(snow+pop size+snow*pop size+CP.mean),f(AoM_2regr[2:7,8+]),sigma(.)*	*49*	*2746.60*	*5591.19*	*0.00*
p(time+leviona),lambda(leviona),phi(sex*Gompertz+sex*[snow+snow*pop size])phi_kid(snow+pop size+snow*pop size+m.mean),f(AoM_2regr[2:7,8+]),sigma(.)	49	2748.13	5594.26	3.07
p(time+leviona),lambda(leviona),phi(sex*Gompertz+sex*[snow+snow*pop size])phi_kid(snow+pop size+snow*pop size+CP.mean),f(AoM_2regr[2:7,8+]),sigma(.)	53	2744.24	5594.47	3.28
p(time+leviona),lambda(leviona),phi(sex*Gompertz+sex*[snow+snow*pop size])phi_kid(snow+pop size+snow*pop size+CP.07),f(AoM_2regr[2:7,8+]),sigma(.)	49	2748.36	5594.71	3.52
p(time+leviona),lambda(leviona),phi(sex*Gompertz+sex*[snow+snow*pop size])phi_kid(snow+pop size+snow*pop size+dNDF24.mean),f(AoM_2regr[2:7,8+]),sigma(.)	49	2748.51	5595.01	3.82
p(time+leviona),lambda(leviona),phi(sex*Gompertz+sex*[snow+snow*pop size])phi_kid(snow+pop size+snow*pop size+NDF.mean),f(AoM_2regr[2:7,8+]),sigma(.)	49	2748.53	5595.06	3.86
p(time+leviona),lambda(leviona),phi(sex*Gompertz+sex*[snow+snow*pop size])phi_kid(snow+pop size+snow*pop size+BGS),f(AoM_2regr[2:7,8+]),sigma(.)	49	2749.27	5596.54	5.35
p(time+leviona),lambda(leviona),phi(sex*Gompertz+sex*[snow+snow*pop size])phi_kid(snow+pop size+snow*pop size+m.max),f(AoM_2regr[2:7,8+]),sigma(.)	49	2750.97	5599.94	8.74
p(time+leviona),lambda(leviona),phi(sex*Gompertz+sex*[snow+snow*pop size])phi_kid(snow+pop size+snow*pop size+Dmax),f(AoM_2regr[2:7,8+]),sigma(.)	49	2754.91	5607.83	16.63
p(time+leviona),lambda(leviona),phi(sex*Gompertz+sex*[snow+snow*pop size])phi_kid(snow+pop size+snow*pop size),f(AoM_2regr[2:7,8+]),sigma(.)	48	2757.06	5610.11	18.92
p(time+leviona),lambda(leviona),phi(sex*Gompertz+sex*[snow+snow*pop size])phi_kid(snow+pop size+snow*pop size+NDVImax),f(AoM_2regr[2:7,8+]),sigma(.)	49	2756.67	5611.34	20.15
p(time+leviona),lambda(leviona),phi(sex*Gompertz+sex*[snow+pop size+snow*pop size])phi_kid(snow+pop size+snow*pop size),f(AoM_2regr[2:7,8+]),sigma(.)	50	2756.22	5612.43	21.24
p(time+leviona),lambda(leviona),phi(sex*[a1+Gompertz]+sex*[snow+pop size+snow*pop size])phi_kid(snow+pop size+snow*pop size),f(AoM_2regr[2:7,8+]),sigma(.)	52	2755.61	5615.22	24.03
p(time+leviona),lambda(leviona),phi(sex*Gompertz+snow+pop size+snow*pop size)phi_kid(snow+pop size+snow*pop size),f(AoM_2regr[2:7,8+]),sigma(.)	47	2760.92	5615.84	24.64
p(time+leviona),lambda(leviona),phi(sex*Gompertz)phi_kid(snow+pop size+snow*pop size),f(AoM_2regr[2:7,8+]),sigma(.)	44	2824.90	5737.79	146.60
p(time+leviona),lambda(leviona),phi(sex*Gompertz)phi_kid(snow+pop size),f(AoM_2regr[2:7,8+]),sigma(.)	43	2833.96	5753.92	162.73
p(time+leviona),lambda(leviona),phi(sex*Gompertz)phi_kid(snow),f(AoM_2regr[2:7,8+]),sigma(.)	42	2839.92	5763.83	172.64
p(time+leviona),lambda(leviona),phi(sex*Gompertz)phi_kid(.),f(AoM_2regr[2:7,8+]),sigma(.)	41	2843.86	5769.72	178.52
p(time+leviona),lambda(leviona),phi(sex*Gompertz)phi_kid(.),f(AoM_regr),sigma(.)	39	2851.97	5781.94	190.75
p(time+leviona),lambda(leviona),phi(sex*Gompertz)phi_kid(.),f(.),sigma(.)	38	2854.37	5784.74	193.55
p(time+leviona),lambda(leviona),phi(sex*Gompertz)phi_kid(.),f(AoM),sigma(.)	57	2837.26	5788.52	197.33

Fig. 2 shows the plot of smoothed estimates of the population counts for the final integrated population model, compared to the observed counts for adult males, adult females, yearlings and kids.

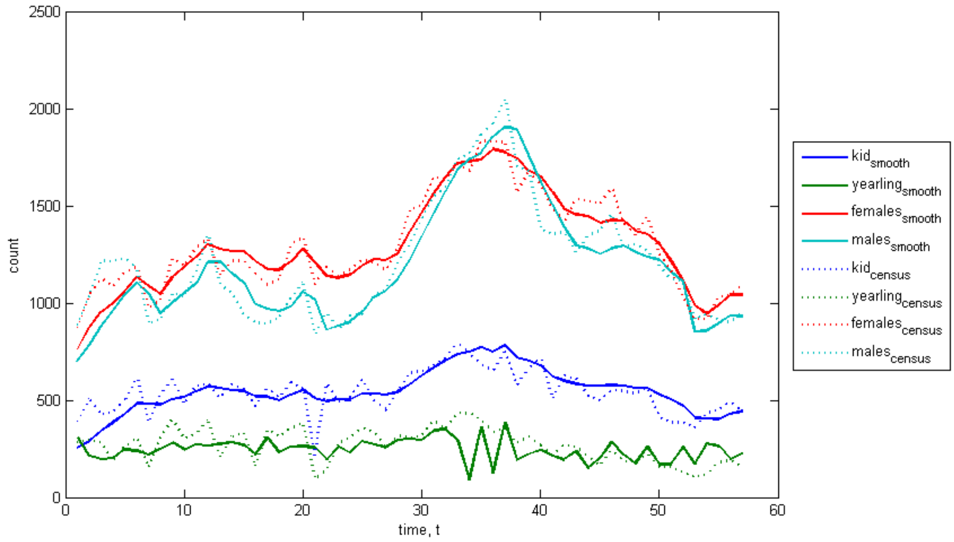

Figure 2. Smoothed integrated model estimates vs observed count census series. Time (t) is number of years since 1956.

The model estimates appear to to have an excellent fit with the observed yearly counts. The integrated population model, including life history information from individually tagged subjects and specifically modeling the variation in age structure of the population, appears thus to describe well the dynamic of the Gran Paradiso Alpine ibex population.

Crude protein content, estimated from NDVI data (Ranghetti, 2014), appears to have a positive effect on kid survival improving the fit of the integrated model (delta AIC =21.24) and confirming previous suggestions that changes in vegetation due to climate change have driven the decline in kid survival in the last 20 years (Pettorelli et al. 2007). Changes in age structure appear instead to affect significantly female productivity. These results are still preliminary and some effects, such as the effect of age of mothers on kid survival have still to be tested. However, our results show that the integrated population modeling approach is a very promising tool to better describe the dynamics and understand the complexly interlinked factors influencing it in the Gran Paradiso National Park Alpine ibex population

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