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Roberta Chirichella
Department of Veterinary Medicine
University of Sassari
via Vienna 2, I-07100 Sassari, Italy
(0039) 079 228667
rchirichella@uniss.it

RH: Chirichella et al. • Alpine chamois population recruitment

Contrasting Effects of Climate Change on Alpine chamois

ROBERTA CHIRICHELLA, [1] *Department of Veterinary Medicine, University of Sassari, via Vienna 2, I-07100 Sassari, Italy*

PHILIP A. STEPHENS, *Department of Biosciences, Durham University, South Road, Durham DH1 3LE, UK*

TOM H. E. MASON, [2] *Department of Biosciences, Durham University, South Road, Durham DH1 3LE, UK*

MARCO APOLLONIO, *Department of Veterinary Medicine, University of Sassari, via Vienna 2, I-07100 Sassari, Italy*

ABSTRACT Global climate change can affect animal ecology in numerous ways, but current researchers usually emphasize undesirable consequences. Temperature increases, for instance, can induce direct physiological costs and indirect effects via mismatches in resource needs and availability. Species living in mountainous regions, however, could experience beneficial effects as winters might become less severe. Here, we examined the potentially opposing effects of climate change during spring, summer, and winter on recruitment in Alpine chamois (*Rupicapra rupicapra*). Using indices of offspring production and survival derived from block count

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[1] *Email: rchirichella@uniss.it*
[2] *Current affiliation: Swiss Ornithological Institute, Seerose 1, CH-6204, Sempach, Switzerland*

censuses performed across a 1,500-km^2 study area in the Italian Alps during summer from 2001 to 2015, we examined initial recruitment (i.e., the ratio of kids to adult females), and first winter survival and net recruitment (i.e., the ratio of yearlings to adult females) of Alpine chamois through the use of linear mixed effects models. Initial recruitment was relatively resistant to the effects of climate change, declining slightly over the study period. We suggest that the effects of increased forage availability and lower snow cover in winter may benefit the reproductive output of adult females, compensating for any negative effects of trophic mismatch and higher temperatures during summer. By contrast, net recruitment strongly declined throughout the study period, consistent with the slight decline of initial recruitment and the negative effects of increasing summer temperatures on the survival of kids during their first winter. These negative effects seemed to outweigh positive effects of climate change, even in a species strongly challenged by winter conditions. These findings provide important information for hunted populations, setting more appropriate hunting bags for yearling chamois. The ecological plasticity of the chamois, however, which also inhabits low altitude, may allow a possible evolutionary escape for the species.

KEY WORDS climate change, ecological plasticity, forage availability, population recruitment, *Rupicapra rupicapra*, winter harshness.

Contemporary climate change affects species in a variety of ways, from altering their spatial distributions (Parmesan and Yohe 2003, Chen et al. 2011, Lenoir and Svenning 2015, Pecl et al. 2017) to changing the timing of events in their annual cycles (Menzel et al. 2006, Fu et al. 2016, Wang et al. 2016, Vitasse et al. 2018). Recently, focus has shifted to looking at the effects of climate change on body condition and the influence of that on population dynamics (Ozgul et al. 2009). The mechanistic processes underlying these responses remain largely unknown, owing to a paucity of long-term data and the lack of an appropriate analytical framework to consider non-stationary distributions in time series (Stenseth and Mysterud 2002, Ozgul et al. 2010). Several researchers have identified temporal trends in body size due to climate change, generally resulting indirectly from changes in resource availability and quality, which affect resource acquisition and growth (Gardner et al. 2011, Sheridan and Bickford 2011).

Such processes could affect population dynamics, and it is important to identify whether and how these factors affect population growth. It is increasingly recognised that the effects of climate changes are not necessarily negative for all species and populations (Pateman et al. 2012, Gullett et al. 2014). In particular, species living in seasonal environments could benefit if winters become less severe (Gonzalez and Crampe 2001, Grotan et al. 2008, Willisch et al. 2013). It is, however, unclear how this may trade-off with changes in spring and summer conditions if high temperatures influence the availability and quality of resources, or the ability of animals to access resources (Weladji et al. 2002). This is especially true for herbivorous vertebrates, which display seasonal reproduction timed to coincide with a highly pulsed peak in resource availability (Post 2003). Ungulates, for instance, exhibit highly synchronous parturition that coincides with the onset of plant growth (Post and Klein 1999, Post et al. 2003). This yields the potential for trophic mismatch between the timing of births and the timing of peak resource availability. Trophic mismatches could have negative consequences for offspring survival, because the energetic demands of lactation, which are typically met by intake of newly emergent plant tissue at peak nutritional value, are the highest of the annual reproductive cycle (Robbins 1983, Clutton-Brock 1991, Post and Forchhammer 2008).

Mountainous areas are hot-spots of very rapid climate change (Diaz and Bradley 1997, Turco et al. 2015). They are, thus, particularly sensitive areas in which to examine the potentially opposing effects of changes in winter, spring, and summer climate on ungulate population recruitment. In these areas, warmer winters are expected to change the rain and snow ratio and elevation boundary, and to increase the frequency of extreme rain-snow events (Beniston and Fox 1996, Inouye et al. 2000, Mysterud et al. 2001, Lapp et al. 2005, Pettorelli et al. 2005*a*). Moreover, the timing of snowmelt should determine the timing of spring vegetation onset and, as the influencing force in habitat use by large herbivores (Fryxell 1991, Albon and Langvatn 1992, Pettorelli et al. 2007), thereby have a pronounced effect on population dynamics of ungulates (Rutberg 1987, Kudo 1991).

The effects of climate change on mountain-dwelling ungulates have been studied, due to the sensitivity of those systems to climate change, and the economic and cultural importance of the ungulates (Apollonio et al. 2010). As yet, however, there is little consensus about whether climate change is likely to have positive or negative effects on mountain ungulates. In this context, evidence for a positive effect of earlier springs comes from studies of chamois (*Rupicapra rupicapra*) in France (Garel et al. 2011), red deer (*Cervus elaphus*) in Norway (Pettorelli et al. 2005*a*), and reindeer (*Rangifer tarandus*; Pettorelli et al. 2005*b*, Helle and Kojola 2008, Tveraa et al. 2013) in Scandinavia. By contrast, it has been suggested that the rate at which new high-quality forage emerges is important for ungulates (Garel et al. 2011, Helle and Kojola 2008). Thus, rapid vegetation green-up affects juvenile growth negatively in bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*), and causes a reduction in juvenile survival of Alpine ibex (*Capra ibex*; Pettorelli et al. 2007). Indeed, the rapid vegetation green-up leads to a shorter period of availability of high-quality forage, decreasing the opportunity for mountain ungulates to exploit it. Moreover, lower reproductive success was revealed in caribou and reindeer due to mismatch between optimal forage conditions and the timing of reproduction (Post et al. 2008, Post and Forchhammer 2008). High temperatures can also reduce foraging activity and can force ungulates to higher elevations (Aublet et al. 2009, Mason et al. 2014, Brivio et al. 2016). As a rule, higher elevations are associated with lower productivity, potentially leading to reduced food intake (Mason et al. 2017).

The Alpine chamois, in the east-central Alps, South-West Trento Province, Italy is a widely distributed Alpine subspecies of chamois currently classified as least concern by the International Union for Conservation of Nature (IUCN) and noted by Corlatti et al. (2011) as the most abundant mountain dwelling ungulate of Europe and the Eastern Asia. This species is experiencing a decrease in some countries in the Alps (Supplemental Material Fig. S1) and is sensitive to temperature (Brivio et al. 2016). Previously, for the same area, Mason et al. (2014) reported a decrease in the body size of yearlings from 1979 to 2010, which was related to increases in mean temperatures and population density.

We take advantage of a long-term dataset to conduct a descriptive study, examining the influence of climatic factors on population recruitment in a mountain ungulate. Our objective was to examine the potentially opposing effects of changes in winter, spring, and summer climate on Alpine chamois population recruitment. We hypothesize these indices of population recruitment can be influenced by environmental and climatic conditions. In particular, we expect a relationship between these indices and forage availability during the birth period and the overall vegetation growing season according to the changing rate at which new forage emerges and the total productivity of meadows during the period of growth for kids; the increasing temperature during the hottest month (i.e., Jul) and the vegetation growing season that can reduce foraging activity and can force ungulates to higher elevations (i.e., areas with lower productivity); and the harshness of the previous winter that can influence the survival rate and have a pronounced effect on population dynamics of mountain dwelling species. We examine evidence for an effect of changing climate on population recruitment, also considering the influence of local population density.

The results from this research can assist with the management of Alpine chamois and provide important information for mountain dwelling species that have very similar ecological and biological characteristics including Chartreuse chamois (*Rupicapra rupicapra cartusiana*), Tatra chamois (*Rupicapra rupicapra tatrica*), Balkan chamois (*Rupicapra rupicapra balcanica*) and Anatolian chamois (*Rupicapra rupicapra asiatica*; Corlatti et al. 2011).

STUDY AREA

The study site (1,432.31 km^2) covered the southwest part of the Province of Trento, East-central Alps, Northern Italy (lat. 46°10′N, long. 10°45′E) and included 7 Alpine chamois management areas (Fig. 1). The climate was typical of Alpine region and could be defined as a transition between the semi-continental and the Alpine climate. Temperature and rain conditions were influenced by the Mediterranean climate in the southern part, while the northern part had a more continental climate. The average winter temperatures were between -5 and -10°C in January and averages of 20-25°C and more in the summer season. Average annual rainfall was 815 mm. Typical evolutions due to current climate changes were documented in the Province of Trento. The average annual temperature increased of 0.6 ± 0.16°C in the last century. In addition, recordings of extreme temperatures were increasingly frequent, with a greater occurrence of summers with temperatures above the average (data from Forecasts and Organization Office - Civil Protection Infrastructures Department of the Province of Trento - www.meteotrentino.it, accessed 15 Jun 2020).

According to snow cover trends, albeit with an extremely irregular pattern (with snowy and dry years), the entire Province of Trento showed a decrease in snow depth of about 5 cm/ year, starting from the late 1980s. As for the number of days with snow on the ground, the trends showed a significant drop at all altitudes, and in particular elevations below 1,200 m, varied between 1-5 days/season. This decrease was more evident in the southern part of this study area and could have high variations based on the exposure (data from Forecasts and Organization Office - Civil Protection Infrastructures Department of the Province of Trento - www.meteotrentino.it, accessed 15 Jun 2020).

Elevations ranged from 65 m above sea level (asl) at the southern border around Lake Garda to 3,558 m asl in the Presanella Massif. The area was forested up to the tree-line at about 2,000 m asl, above which it consisted of Alpine meadows, rocky outcrops, scree fields and open rock faces. Typically, meadows in siliceous areas were dominated by scabrous culm fescue (*Festuca scabriculmis*) and Alpine sedge (*Carex curvula*), whilst those in calcareous areas were composed of blue moor-grass (*Sesleria albicans*) and carnation grass (*Carex firma*). In these areas the mountainous terrain achieves a rugged nature.

Among the chamois management areas, Adamello, Destra Chiese and Presanella were characterised by nutrient-poor siliceous vegetation, and Brenta, Cadria Altissimo, Misone-Casale and Ledro were characterised by nutrient-rich calcareous vegetation (Chirichella et al. 2012). According to a genetic investigation made in the same hunting districts (Azzu 2019), chamois living in different management areas showed individual genetic signatures, suggesting that they were independent units (M. Scandura, Department of Veterinary Medicine - University of Sassari - Italy, unpublished data). In these areas chamois were hunted with rifles every year between mid-September and late-December. Hunting was strictly regulated through licenses issued by local wildlife boards. Area-wide hunting quotas were set for specific age classes in each sex (Mason et al. 2011, Chirichella et al. 2012, Mason et al. 2014). In our study site, harvesting plans consisted of 3 age classes for males (i.e., yearlings, 2-5, ≥ 6 years of age) and females (i.e., yearlings, 2-10, ≥ 11 years of age). Hunting of kids did not occur in the hunting districts.

In addition to Alpine chamois, large herbivores included red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), European mouflon (*Ovis gmelini musimon*) and Alpine ibex (*Capra ibex*). Potential terrestrial predators included a small and yet stable population of brown bears (*Ursus arctos*), a small number of lynx (*Lynx lynx*), and occasional wolves (*Canis lupus*; Groff et al. 2016). The golden eagle (*Aquila chrysäetos*, Pedrini et al. 2005) was the only avian predator, potentially preying upon chamois kids in their first weeks of life. Eagle presence was stable throughout the study period (Adamello Brenta Nature Park 2011) but the influence of eagle predation on Alpine chamois populations was negligible (Haller 1996).

METHODS

Data Collection

We derived 2 indices of Alpine chamois population recruitment: initial recruitment (i.e., the ratio of kids to adult females [NK:NF]) and net recruitment (i.e., ratio of yearlings to adult females [NY:NF]). When modelling net recruitment, we also used the ratio of kids to adult females in the previous year as a potential predictor. These indices were derived from block count censuses in 2001-2015, carried out during July – mid-August (i.e., after the birth period) in all municipal reserves (92 management units; area [$\bar{x}$ ± SE]: 15.55 ± 1.72 km^2; Fig. 1) of the 7 hunting districts in the South-West part of Trento province (Fig. 2). The block count census method (Corlatti et al. 2015) entailed a coordinated and simultaneous count of all individuals across the different blocks of each hunting district during their peak of activity (i.e., the first 4 hrs after sunrise; Cederlund 1989, Green and Bear 1990, Aublet et al. 2009). Within each block of our study area, pairs of rangers with prior experience with Alpine chamois in the area to scan performed the counts (452 blocks in the study site) in open habitats when the weather was favorable (i.e., good visibility, lack of strong wind, rain, and snow).

Each pair of observers was in radio contact with the observers of the nearby monitoring areas and had binoculars, spotting scopes, and appropriate maps. The monitoring blocks and the applied techniques remained constant throughout the study period. Despite the good visibility offered by open areas and the use of census monitoring in favourable weather conditions, the rugged nature of the mountainous terrain, due to the presence of rocks, cliffs, ridges and valleys, may restrict the ability to detect animals (Gaillard et al. 2003, Loison et al. 2006, Corlatti et al. 2015). Data were reported for each municipal reserve and aggregated into 50 units where the species showed a stable and constant presence throughout the summer and autumn season (natural barriers such as the top and bottom of the valleys, roads, and other artificial components which either prevent or strongly limit movement of animals between one area and another). Our estimates of kids, yearlings, and adult females were based on sufficient counts in all units to allow unbiased estimates of recruitment (Garin and Herrero 1997, Albon et al. 2000, Herrero et al. 2001, Antonucci et al. 2011). Counts of kids, yearlings, and adult females ranged from 94-320 among these 50 units. We followed all applicable institutional or national guidelines for the care and use of animals (guidelines for block count censuses: decision n. 137 of Trento Province Government / 4 Feb 2011; decree of the Director of Forest and Wildlife Service of Trento Province n. 276 / 4 Jul 2011).

A range of climatic and non-climatic factors are expected to influence chamois population recruitment indices. To investigate potential effects of population density, site-specific population density estimates were used from summer censuses conducted throughout the study. We assumed that density estimates from this time of year (typically Jul) would reflect the population density over the late spring and summer period.

To characterise variation in the productivity and phenology of Alpine meadows during the vegetation growing season (Table 1, Fig. 2) and the birth period, we used normalised difference vegetation index (NDVI) data from MODIS (MOD13Q1; https://LPDAAC.usgs.gov, accessed 8 May 2020). These data are available at 16-day intervals at a 250 m resolution. We derived NDVI only for cells completely included in meadows land use class of the Corine Land Cover map (294.69 km^2, corresponding to the 20.57% of the entire study site; http://land.copernicus.eu/pan-european/corine-land-cover/clc-2012, accessed 8 May 2020). Remote sensing NDVI time series are highly correlated with single point ground measurements and therefore accurately represented growth dynamics of alpine grassland (e.g., Fontana et al. 2008).

To investigate a possible direct thermoregulatory link between climate and population recruitment, we calculated yearly, site-specific estimates of mean daily maximum temperature during the hottest month (i.e., Jul) and the vegetation growing season and mean daily minimum temperature during snow cover period between 2000 and 2015 from 5 weather stations (Forecasts and Organization Office - Civil Protection Infrastructures Department of the Province of Trento - www.meteotrentino.it, accessed 15 Jun 2020). Mean daily maximum and minimum temperature was derived through co-interpolation with digital elevation model (DEM) methods and zonal statistics (ArcGIS 10 Geostatistical Analyst Tools and Spatial Analyst Tool; Supplemental Material Fig. S2) for each of the hunting management units.

We used extent and duration of snow cover to investigate the effects of winter harshness on female productivity (initial recruitment) and kid survival (net recruitment) during their first winter. Snow cover extent was the average of maximum snow cover in each hunting unit (i.e., the mean area covered by snow between Nov and early May) while snow cover duration was the number of days between November and early May on which maximum snow cover extent was ≥ 50%, based on the index of snow cover presence available at 8 day intervals (i.e., duration was reported to the nearest 8 days) at 500 m resolution (MOD10A2; Hall et al. 2006; http://modis-snow-ice.gsfc.nasa.gov, accessed 8 May 2020; Table 1).

Previous researchers in the study area demonstrated contrasting life histories and horn growth among neighbouring chamois populations located in areas of different geological substrate (Mason et al. 2011, Chirichella et al. 2012). Consequently, we also tested for the influence of substrate (calcareous vs. siliceous) on population recruitment.

We defined the bounds of the vegetation growing season as the period between the snow-melt in spring, when snow cover was reduced to the minimum value (which generally occurs between late Mar and early May), and the first significant snowfall in winter that results in new snow settling on the ground (which generally occurs between early Nov and late Dec; Mason et al. 2014, Fig. 2).

Data Analysis

We described the trend of both indices of recruitment throughout the study period across the whole study area by means of regression lines and we used t-tests to compare the ß coefficients of initial and net recruitment. We used linear mixed effects models (LMM) to identify the major influences of recruitment, implemented with the lme function of the nlme package in R and fitted using maximum likelihood (Pinheiro et al. 2016). We used hunting district (*n* = 7) as a random factor and explored responses among the 50 different management units (Machlis et al. 1985). We *z*-transformed continuous independent variables to compare the relative effects of predictors on population recruitment.

We fitted models testing both initial recruitment, with the NK:NF ratio as the dependent variable, and net recruitment, with the NY:NF ratio as the dependent variable. We fitted models with all possible biologically meaningful combinations of independent variables. We assessed collinearity using variance inflation factors (VIFs), dropping any models with VIFs > 3 (Zuur et al. 2010). Through the examination of residual plots we accounted for temporal autocorrelation in our data and we added a first order autocorrelation structure (corAR1) to remove it (i.e., the residuals randomly scattered about zero).

We used Akaike's information criterion (AIC; Burnham and Anderson 2002) to select the best fitting sets of models. We selected all models within 6 AIC units of the best fitting model (i.e., ΔAIC ≤ 6, indicating substantial and moderate evidence to support the candidate model; Burnham and Anderson 2002, Richards 2008, Burnham et al. 2011). The final sets of models obtained were then refitted using restricted maximum likelihood estimation, to have a better estimate of variance components in models with random effects (Bolker et al. 2009). We checked assumptions of normality, homoscedascity, and independence by inspecting standardised residual plots (Zuur et al. 2009). We assessed model goodness-of-fit using marginal R^2 (R^2_m, the variance explained by fixed factors) and conditional R^2 (R^2_c, the variance explained by both fixed and random factors) for mixed effect models (Nakagawa and Schielzeth 2013, Johnson 2014). Statistical analyses were performed in R version 3.4.4 (R Core team 2018).

RESULTS

Both indices of recruitment declined throughout the study period across the whole study area, showing a reduction of 5% (from 75% to 70% of females with kids) for initial recruitment and of 17% (from 56% to 39% of females with yearlings) for net recruitment (NK:NF, regression line [ß = -0.004]: $F_{1,746} = 18.01$, $P < 0.01$; $R^2 = 0.02$; NY:NF, regression line [ß = -0.012]: $F_{1,746} = 127.90$, $P < 0.01$; $R^2 = 0.15$; Fig. 3). Net recruitment was significantly more affected than initial recruitment ($t = 3.795$, $P < 0.001$). The average top models ($\Delta AIC \leq 6$; $R^2m = 0.44$; $R^2c = 0.57$) explaining the variation in initial recruitment included 7 variables, 4 of which with significant effects (Table 2). Initial recruitment was associated most strongly with environmental and climatic conditions experienced during the gestation and lactation periods. Forage availability (i.e., NDVI) across the whole growing season (3% for each 0.1 value of NDVI) was positively associated with NK:NF. In particular, forage availability during May and June (during the year of birth and the year prior to birth, 0.05% and 4% respectively for each 0.1 value of NDVI) resulted in an increase of NK:NF.

In contrast, we detected a negative association between mean daily maximum temperature experienced by mothers during the growing season and initial recruitment (-1% for an increase of 5°C;Table 2, Fig. 4A). Despite mean forage availability during the growing season remaining stable over the study period (linear regression: ß = 2.11, $F_{1,746} = 1.75$, $P = 0.15$; $R^2 < 0.001$), forage availability at the birth peak has declined over the study period (regression line [ß = -5.75]: $F_{1,746} = 47.13$, $P < 0.01$; $R^2 = 0.06$; Supplemental Material Fig. S3), showing an earlier spring green-up of the land surface (anticipation of the 16 days period in which there was the major frequency of the highest maximum NDVI; Supplemental Material Fig. S4).

According to the net recruitment, despite the absence of a clear best model in the model selection procedure (Supplemental Material Table S1), the average top models ($\Delta AIC \leq 6$; $R^2m = 0.44$; $R^2c = 0.55$) included 9 variables, 5 of which with significant effects (Table 3). This index was, unsurprisingly, positively correlated with initial recruitment (Table 3, Fig. 4). Net recruitment was also positively associated with the forage availability experienced over the entire vegetation growing season (4.5% for each 0.1 value of NDVI), and negatively associated with the temperature during summer (i.e., Jul; -1% for an increase of 4°C), winter harshness (i.e., snow cover extent; 4.5% for a snow cover extent reduction of 10%) and local chamois density (-5% for a local density increase of 5 individuals/100 ha; Table 3, Fig. 4B). Population density aside (linear regression: $ß = 0.08$, $F_{1,746} = 7.35$, $P = 0.01$, $R^2 = 0.01$), only the mean of daily maximum temperature during July steadily increased during the study period (linear regression: $ß = 0.34$, $F_{1,746} = 40.82$, $P < 0.01$; $R^2 = 0.05$; Supplemental Material Fig. S3).

DISCUSSION

Animals occupying seasonal environments often face contrasting effects of global change (Albon et al. 2017). Rising temperatures are likely to lead to milder winters but also to reduced forage availability during the season of offspring production and rearing. It means that the lack of synchronization between the timing of peak resource availability and the timing of peak birth dates could affect individual fitness and have consequences for population demography, reducing cohort-specific survival (e.g., a roe deer population in eastern France showed a lack of response in parturition date to the increasingly early availability of high-quality resources, Plard et al. 2014). Increases in temperature can also present problems for thermoregulation, impacting activity budgets and altitudinal distribution (Brivio et al. 2016, Mason et al. 2017). Seasonal differences in the directions of these effects make it difficult to predict the cumulative effects of climate change on the population dynamics of species in seasonal environments.

In mountainous regions such as the European Alps, climate change is expected to accelerate during the 21st century, leading to seasonal shifts in cycles of precipitation, global radiation, relative humidity, changes in temperature and precipitation extremes, strong decreases in winter snow cover, and increases in winter temperature (Gobiet et al. 2014). These changes are typical for the Alpine region and are also documented for the Province of Trento. For Alpine chamois, variation in initial recruitment was associated most strongly with environmental and climatic conditions experienced during the gestation and lactation periods. In particular, initial recruitment depended on forage availability during May and June in the year of birth and the forage availability experienced by mothers during the entire growing season in the year before births. Net recruitment was similarly affected by forage availability during the growing season. While winter harshness negatively influenced net recruitment, winters have not reduced in severity sufficiently to offset the negative effects on kid survival at higher temperatures.

Contrasting Effects of Climate Change

We demonstrated the effects of environmental factors acting at 3 different times of the life cycle: the availability of forage during and immediately after the birth period, summer temperatures, and the harshness of the first winter experienced by new recruits. Consistent with much of Europe (including the boreal region; Garonna et al. 2014), the peak in NDVI no longer coincides with the period of births, which could be negatively effecting kid survival (Supplemental Material Fig. S3, S4). If chamois are unable to adapt phenologically to these changes, the timing of peak resource availability may fail to match the timing of peak energy expenditure. This point has been examined in large herbivores (Post and Forchhammer 2008); where reproduction is triggered by day length rather than resource availability, adaptive responses in the timing of births are unlikely (Plard et al. 2014).

Higher daily temperatures during summer may lead to chamois kids spending more time resting and less time foraging, which could affect their ability to store energy reserves and invest in growth. Indeed, chamois, like many ungulates, reduce their feeding activity during the hottest period of the day (Ruttimann et al. 2008, Mason et al. 2014, Mason et al. 2017). Furthermore, chamois spend less time foraging when it is hotter, independent of time of day (Mason et al. 2014). Our results suggest that increasing temperatures could limit the ability of kids to acquire resources, limiting their ability to store the body reserves required to survive the following winter (Mason et al. 2014).

Given the clear increasing temperature trend currently underway in the Alpine region, (Supplemental Material Fig. S3), the negative effect of higher temperatures on net recruitment could become a limiting factor in the population dynamics of this species in the future.

High levels of snowfall, resulting in long lasting snow cover in winter, also negatively affected the survival of young. Our data showed that this species is very sensitive to large swings in winter snow conditions. In line with previous studies on Alpine chamois (Loison et al. 1999, Jonas et al. 2008, Willish et al. 2013) and other mountain ungulates (Crampe et al. 2002, Gonzalez and Crampe 2001, Grotan et al. 2008, Jacobson et al. 2004), we revealed that snow conditions during the winter are important for population recruitment. Yearling survival can fluctuate in response to variation in the duration of snow cover, which affects foraging conditions in the lead up to winter (Gaillard et al. 1998, van de Kerk et al. 2018). In contrast to summer temperature, there was no clear temporal trend in snow cover, which might have compensated for negative effects of climate change on this species (Supplemental Material Fig.

S3). According to winter condition we also have to consider that in our study area, collinearity occurred among snow cover duration, snow cover extent, and mean daily minimum temperature during winter season. All of these variables were correlated and thus help explain winter harshness, and we included the variable among them that accounted for most variation in each model prediction.

Different Sensitivity to Changing Conditions in Adults and Young

Despite substantial inter-annual environmental variability, the productivity of adult females (initial recruitment) has remained relatively stable over time, likely indicating an unchanged ability of females to attain high levels of body condition. High forage availability during May and June, and throughout the growing season (i.e., late Mar-Nov), was positively related to initial recruitment, suggesting that mothers benefit from favourable foraging conditions during parturition and nursing. The mean daily maximum temperature to which mothers were exposed during the vegetation growing season preceding the gestation period was negatively associated with initial recruitment, but weakly so. It is accepted that reproductive potential depends on the body condition of females (Garel et al. 2009), which influences their ability to regulate their energetic balance by increasing food intake, catabolizing fat reserves and proteins, or reducing the energy allocated to other activities (Chan-McLeod et al. 1994, Parker et al. 2009, Monteith et al. 2013).

Increasing temperature can disrupt activity patterns and habitat selection in mountain ungulates, forcing them to higher elevations where forage is of lower quality or scarcer (Brivio et al. 2016, Mason et al. 2017). Despite decreasing forage condition during the birth peak (Supplemental Material Fig. S3) and documented warming throughout the Alpine region (Gobiet et al. 2014), adult females were mostly able to compensate for these shortcomings, resulting in only slight declines in initial recruitment. By contrast, net recruitment, which reflects the survival of kids during their first year of life, decreased substantially during the study, suggesting lower adaptability of younger animals to ongoing global change. Indeed, as reported by Mason et al. (2014), the body mass of yearlings in the study area have undergone pronounced declines, associated with concurrent increases in temperature and population density, but not forage productivity. Here, we reveal a connection between increasing temperatures and the net recruitment in these populations, showing a clear, negative effect on population trends of a mountain dwelling mammal. Large herbivore population dynamics are typically characterized by constant adult survival and variable recruitment (Gaillard et al. 1998). We show that the primary influence of declines in recruitment in a mountain dwelling ungulate is the (decreasing) survival of young, rather than changes in female productivity.

Considering our findings, it appears likely that the decreasing trend of Alpine chamois in most well-established, high-altitude populations will continue and could spread to other areas as climate change progresses. The ecological plasticity of this species, which also inhabits low altitude and wooded areas (Schröder and von der Marlsburg 1982, Schröder 1983), could point to a possible evolutionary escape for the species. The effects of climate change are likely to be quite different in such environments, where chamois may be able to profit from favorable local microclimatic conditions in dense forest. Indeed, low altitude populations of chamois have increased locally and Alpine chamois have spread in low altitude environments (Apollonio et al.

2010). Flexibility in habitat use could provide an important means by which mountain dwelling species can buffer the effect of climate change.

MANAGEMENT IMPLICATIONS

Our results indicate that managers need to consider the effects of climate change in hunter harvest designs for Alpine chamois. Reductions in initial and net recruitment from climate change may reduce the number of individuals available for harvest to meet population objectives. This is especially true for yearling harvest that must decrease in line with the decrease of net recruitment. Annual monitoring of recruitment thus provides essential information for understanding and managing population dynamics in relation to a changing climate, and how best to adjust hunter harvest to meet population objectives.

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Associate Editor:

Figure Captions

Figure 1. The study area (1,432.31 km^2) in the Province of Trento, central-eastern Alps, Italy (AT = Austria; CH = Switzerland; FR = France; IT = Italy; SI = Slovenia). The 7 hunting districts (black lines; substrate type: [s] = siliceous, [c] = calcareous) and their subdivision into municipal reserves (white lines), where we conducted summer block count censuses from 2001 to 2015. Darker colours correspond to higher elevation above sea level.

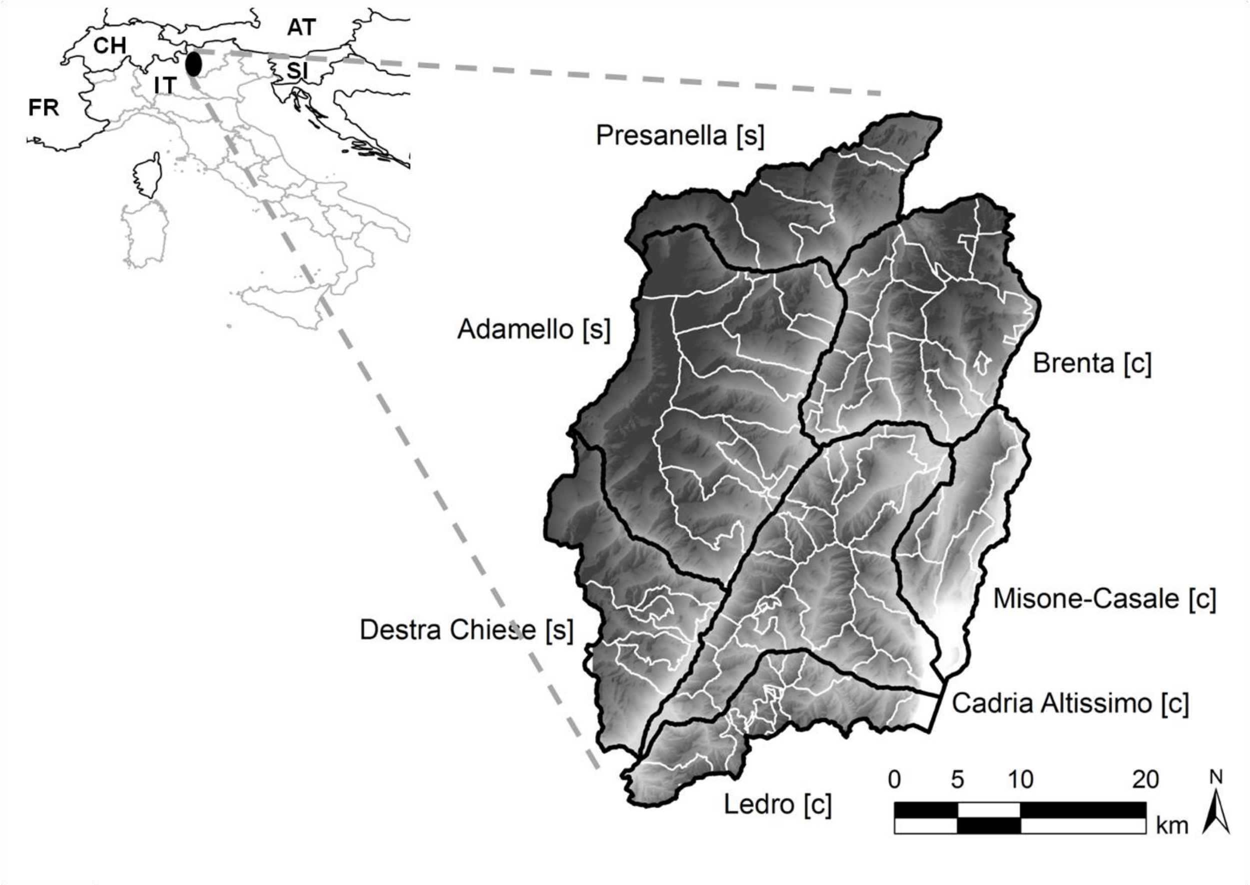

Figure 2. Life cycle and periods of data collection for Alpine chamois in the Province of Trento, central-eastern Alps, Italy. The vegetation growing season (and its complement, the snow cover period) was defined as the period between the snow-melt in spring (which generally occurs between late Mar and early May) and the first significant snowfall in winter that results in new

snow settling on the ground (which generally occurs between early Nov and late Dec). Dark green and blue indicate respectively the most intensive growing period for the vegetation and the most relevant snow cover period in the 2001-2015 interval. Dark grey indicates the period in which most births and matings occur in the Alps.

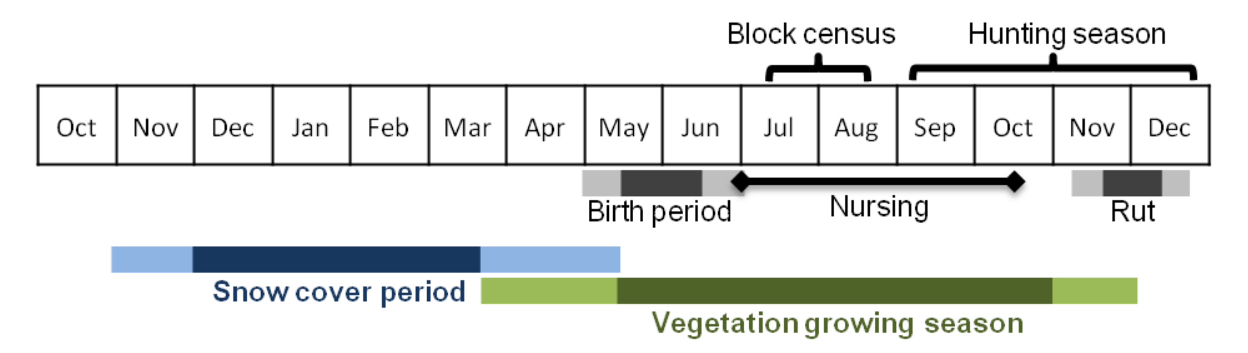

Figure 3. Mean Alpine chamois population recruitment in the Province of Trento, central-eastern Alps, Italy, 2001-2015, expressed as the kids to adult females ratio (NK:NF; panel A; regression line [ß = -0.004]: $F_{1,746} = 18.01$, $P < 0.01$; $R^2 = 0.02$) and the yearlings to adult females ratio (NY:NF; panel B; regression line [ß = -0.012]: $F_{1,746} = 127.90$, $P < 0.01$; $R^2 = 0.15$). Each point represents one of the 50 aggregated hunting units used in analysis. Gray-shaded areas show standard error intervals.

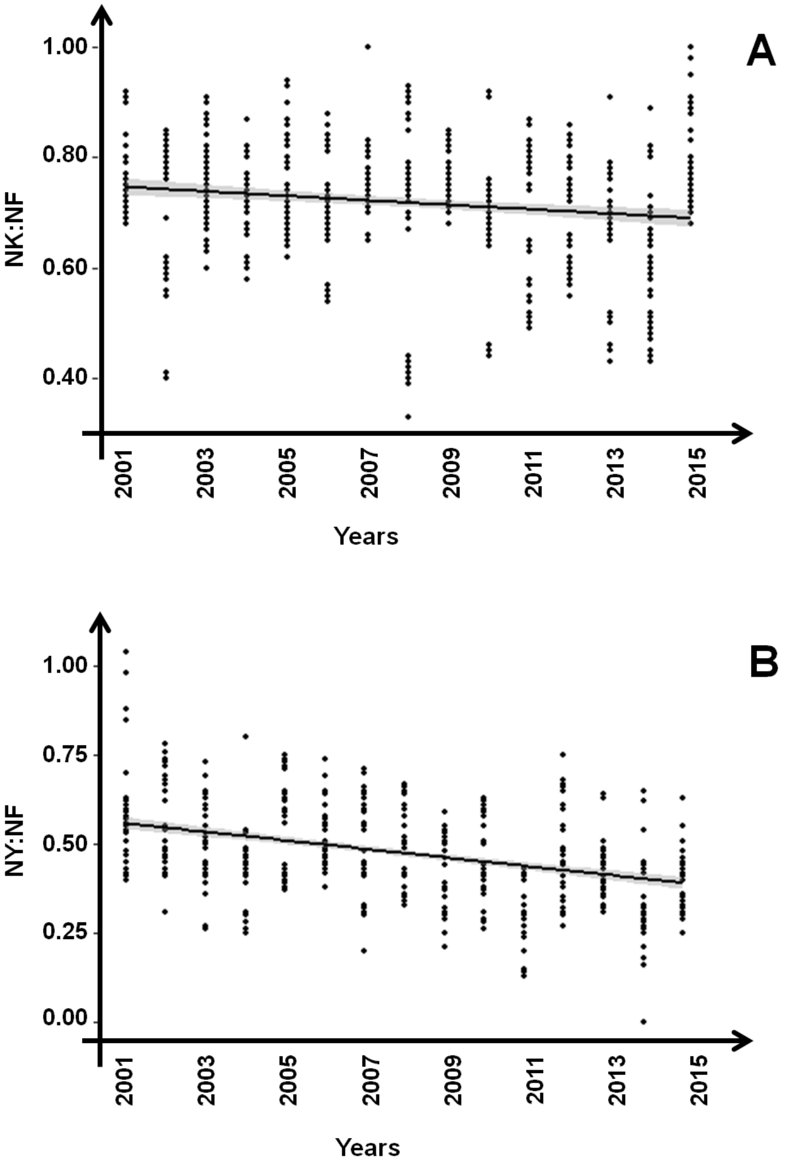

Figure 4. Predicted effects of key independent variables on NK:NF (kids/adult females, panel A) and NY:NF (yearlings/adult females, panel B) from the final set of linear mixed effect models in the Province of Trento, central-eastern Alps, Italy (1,432.31 km^2), 2001 and 2015. Solid lines are predictions of the most parsimonious model for each ratio, with other predictors set to mean values. Gray-shaded areas show standard error intervals. NDVI = normalised difference vegetation index.

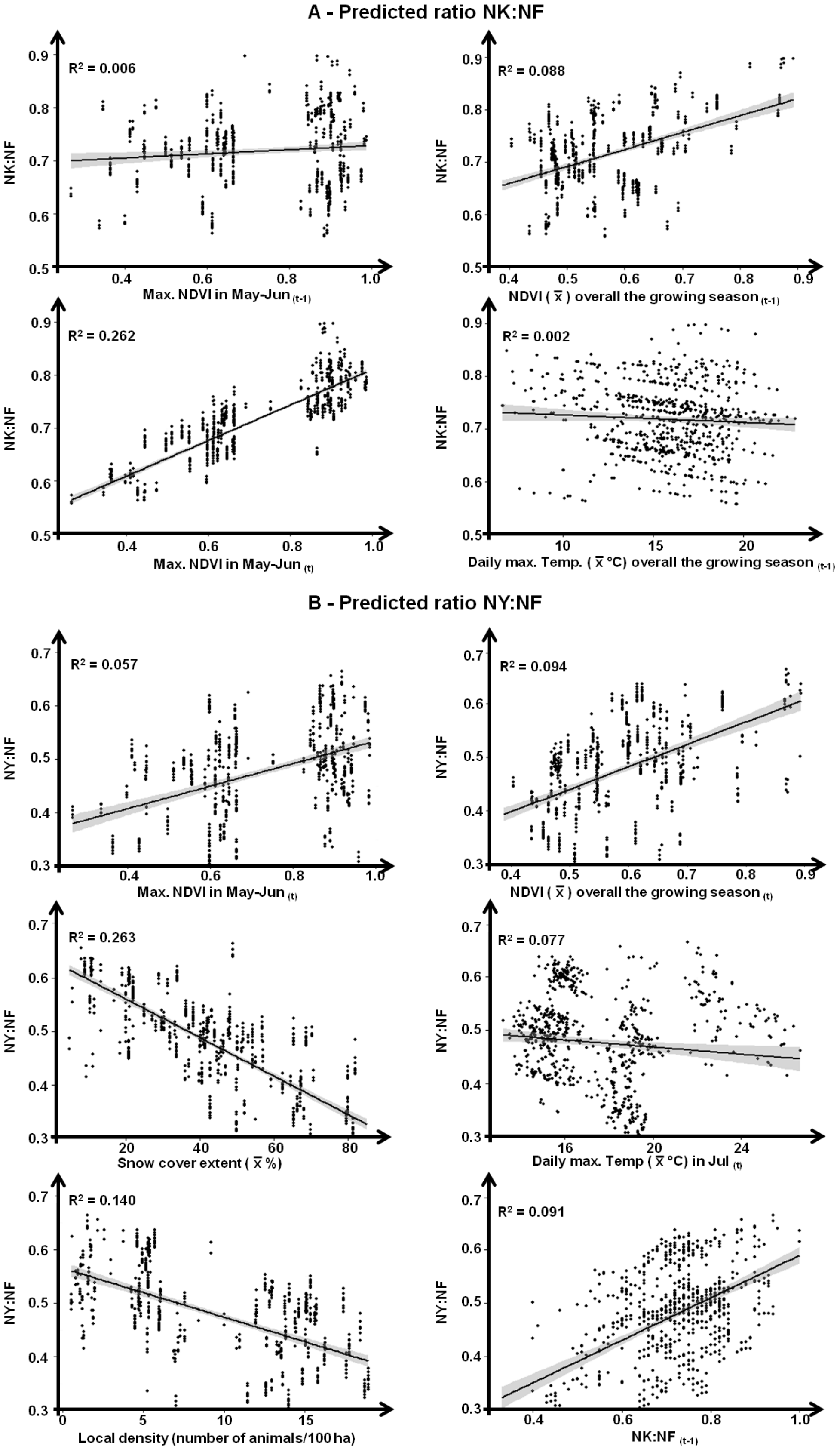
A - Predicted ratio NK:NF
R² = 0.006
NK:NF
Max. NDVI in May-Jun (t-1)
R² = 0.088
NK:NF
NDVI (x̄) overall the growing season (t-1)
R² = 0.262
NK:NF
Max. NDVI in May-Jun (t)
R² = 0.002
NK:NF
Daily max. Temp. (x̄ °C) overall the growing season (t-1)
B - Predicted ratio NY:NF
R² = 0.057
NY:NF
Max. NDVI in May-Jun (t)
R² = 0.094
NY:NF
NDVI (x̄) overall the growing season (t)
R² = 0.263
NY:NF
Snow cover extent (x̄ %)
R² = 0.077
NY:NF
Daily max. Temp (x̄ °C) in Jul (t)
R² = 0.140
NY:NF
Local density (number of animals/100 ha)
R² = 0.091
NY:NF
NK:NF (t-1)

Table 1. Potential predictors of Alpine chamois population recruitment the 1,432.31 km^2 Province of Trento, central-eastern Alps, Italy, 2001 and 2015. NK:NF is the ratio of kids to adult females (i.e., initial recruitment); NY:NF is the ratio of yearlings to adult females (i.e., net recruitment).

			Dependent variable	
Independent variable	**Description**	**Period of data collection**	**NK:NF**[a]	**NY:NF**[b,c]
BIRTH_MAX_NDVI_t [d]	Max. NDVI (normalised difference vegetation index) value for Alpine meadows during birth period (16 day intervals at 250 m resolution)	May-Jun - season t	x	x
BIRTH_MAX_NDVI_t-1[d]	Max. NDVI value for Alpine meadows during birth period (16 day intervals at 250 m resolution)	May-Jun - season t-1	x	
M_NDVI_t[d]	NDVI value ($\bar{x}$) for Alpine meadows overall the vegetation growing season (16 day intervals at 250 m resolution)	Late Mar-Nov - season t		x
M_NDVI_t-1[d]	NDVI value ($\bar{x}$) for Alpine meadows overall the vegetation growing season (16 day intervals at 250 m resolution)	Late Mar-Nov - season t-1	x	x

TEMP_JULY_t-1[e]	Jul daily max.temp. ($\bar{x}$)	Jul – season t-1		x
TEMP_t[e]	Vegetation growing season daily max. temp. ($\bar{x}$)	Late Mar-Nov - season t		x
TEMP_t-1[e]	Vegetation growing season daily max. temp. ($\bar{x}$)	Late Mar-Nov - season t-1	x	
SNOW COVER EXTENT[f]	Max. snow cover extent ($\bar{x}$) in percentage derived from a remote index of snow cover presence (8 day intervals data at 500 m resolution were averaged for each hunting unit)	Nov-Early May period	x	x
SNOW COVER DURATION[f]	Number of days in which max. snow cover extent in percentage derived from a remote index of snow cover presence (8 day intervals at 500 m resolution) was ≥ 50%	Nov-Early May period	x	x
TEMP_WIN_t[e]	Winter daily min. temp. ($\bar{x}$)	Nov-Early May period - season t		x
TEMP_WIN_t-1[e]	Winter daily min. temp. ($\bar{x}$)	Late Mar-Nov - season t-1	x	
DENSITY[g]	Number of animals/100 ha	Mid Jul-mid Aug	x	x
SUBSTRATE	[c] = calcareous; [s] = siliceous	-	x	x

a = NK:NF is the ratio of kids to adult females (initial recruitment).

b = NY:NF is the ratio of yearlings to adult females (net recruitment).

c = As predictor of this independent variable was considered even the NK:NF ratio in the season t-1. When not available from census data, we calculated the same ratio by using standard monitorings (i.e., data collected from vantage points/small transects in the ungulate monitoring project inside the Adamello Brenta Nature Park and fieldwork surveys done by Forest and Wildlife Service of the Province of Trento and the Trento provincial hunting association in the surrounding areas) (see Methods section for major details).

d = Data availability: MOD13Q1 - https://LPDAAC.usgs.gov, accessed 8 May 2020.

e = Data availability: Data from 10 weather station (Forecasts and Organization Office - Civil Protection Infrastructures Department of the Province of Trento - www.meteotrentino.it, accessed 15 Jun 2020) were used to derive a grid (250×250 m) through kriging co-interpolation with Digital Elevation Model and mean values for each hunting unit were calculated through zonal statistics (ArcGIS 10 Spatial Analyst Tool).

f = Data availability: MOD10A2 - http://modis-snow-ice.gsfc.nasa.gov, accessed 8 May 2020.

g = Data availability: Hunting Association of the Province of Trento.

Table 2. Parameter estimates (ß), standard errors (SE), 95% Confidence Intervals (CIs) and *P*-value of the average top models (Δ Akaike's information criterion [AIC] ≤ 6; $R^2m = 0.44$; $R^2c = 0.57$) explaining the variability of the kids to adult females ratio (NK:NF, initial recruitment) throughout the southwest part of Trento province (1,432.31 km^2 study area, Central-Eastern Alps, Italy), 2001 and 2015. Variables in bold showed significant effects.

Parameter	**ß**	**SE**	**CIs**		***P***
			Lower	**Upper**	
Intercept	**0.7194**	**0.0205**	**0.1538**	**0.2342**	**<0.0001**
BIRTH_MAX_NDVI_t-1 [a]	**0.0106**	**0.0037**	**0.0034**	**0.0179**	**0.0040**
BIRTH_MAX_NDVI_t [b]	**0.0680**	**0.0038**	**0.0608**	**0.0752**	**<0.0001**
M_NDVI_t-1 [c]	**0.0326**	**0.0047**	**0.0238**	**0.0418**	**<0.0001**
TEMP_t-1 [d]	**-0.0157**	**0.0045**	**-0.0246**	**-0.0069**	**0.0005**
DENSITY [e]	0.0003	0.0050	-0.0001	0.0010	0.5143
SNOW COVER DURATION [f]	-0.0002	0.0042	-0.0008	0.0008	0.5934
SUBSTRATE [c] [g]	-0.0010	0.0191	-0.0384	0.0363	0.4369

a = Max. NDVI (normalised difference vegetation index) value for Alpine meadows during birth period (May-Jun - season t-1).

b = Max. NDVI value for Alpine meadows during birth period (May-Jun - season t).

c = NDVI value ($\bar{x}$) for Alpine meadows overall the vegetation growing season (Late Mar-Nov - season t-1).

d = Vegetation growing season daily max. temp. ($\bar{x}$; Late Mar-Nov - season t-1).

e = Alpine chamois local density (Number of animals/100 ha).

f = Number of days in which max. snow cover extent in percentage during Nov-Early May period was ≥ 50%.

g = Geological substrate ([c] = calcareous; [s] = siliceous)..

Table 3. Parameter estimates (ß), standard errors (SE), 95% Confidence Intervals (CIs) and *P*-value of the best model (Δ Akaike’s information criterion [AIC] ≤ 6; $R^2m = 0.44$; $R^2c = 0.55$) explaining the variability of yearlings to adult females ratio (NY:NF, net recruitment) overall the southwest part of Trento province (1,432.31 km^2 study area, Central-Eastern Alps, Italy) between 2001 and 2015. Variables in bold showed significant effects.

Parameter	**ß**	**SE**	**CIs**		***P***
			Lower	**Upper**	
Intercept	**0.4409**	**0.0314**	**0.3794**	**0.5024**	**<0.0001**
BIRTH_MAX_NDVI_t [a]	0.0102	0.0061	-0.0018	0.0222	0.2557
M_NDVI_t [b]	**0.0238**	**0.0064**	**0.0113**	**0.0363**	**0.0007**
M_NDVI_t-1 [c]	0.0072	0.0068	-0.0061	0.0205	0.1735
TEMP_JULY_t-1 [d]	**-0.0580**	**0.0080**	**-0.0737**	**-0.0423**	**<0.0001**
TEMP_t [e]	0.0062	0.0059	-0.0054	0.0178	0.4229
SNOW COVER EXTENT [f]	**-0.0298**	**0.0086**	**-0.0467**	**-0.0129**	**<0.0001**
DENSITY [g]	**-0.0356**	**0.0167**	**-0.0683**	**-0.0029**	**<0.0001**
SUBSTRATE [c] [h]	0.0751	0.0377	0.0012	0.1490	0.1727
NK:NF_t-1 [i]	**0.0331**	**0.0048**	**0.3794**	**0.5024**	**<0.0001**

a = Max. NDVI (normalised difference vegetation index) value for Alpine meadows during birth period (May-Jun - season t).

b = NDVI value ($\bar{x}$) for Alpine meadows overall the vegetation growing season (Late Mar-Nov - season t).

c = NDVI value ($\bar{x}$) for Alpine meadows overall the vegetation growing season (Late Mar-Nov - season t-1).

d = Jul daily max.temp. ($\bar{x}$;season t-1).

e = Vegetation growing season daily max. temp. ($\bar{x}$; Late Mar-Nov - season t).

f = Max. snow cover extent ($\overline{x}$) in percentage during Nov-Early May period.

g = Alpine chamois local density (Number of animals/100 ha).

h = Geological substrate ([c] = calcareous; [s] = siliceous).

i = NK:NF ratio (initial recruitment) in the season t-1.

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Summary for the electronic version of the table of contents:

Describing the potentially opposing effects of climate change during spring, summer, and winter on population recruitment in Alpine chamois, we revealed a decrease in survival of kids during their first winter during the study period. Therefore, it is important to set appropriate upper limits on yearling harvest in management plans or in extreme case to exclude them at all, in accordance to their increasing reduction in the population. This research provides for precautions in the management of Alpine chamois and can also provide important information for mountain dwelling species and subspecies with similar ecological and biological characteristics.