Influence of migratory ungulate management on competitive interactions with resident species in a protected area

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Abstract.   Migratory animals can represent links between protected and unprotected parts of their home ranges. Management of such species outside a conservation area can influence species interactions inside the protected zone. This may result in unintended effects on populations of conservation concern even if they spend their entire life cycle within the protected area. We examined interspecific interactions between three species of large herbivores in the absence of mammalian predators in the Swiss National Park, and assessed whether the population size of the migratory red deer (*Cervus elaphus*) that is harvested outside the park in autumn and winter affected the two resident species, chamois (*Rupicapra rupicapra*) and ibex (*Capra ibex*). Dietary overlap was high between the three species while they co-occurred in the park, suggesting potential for interspecific resource competition. Particularly the habitat use of chamois was affected by red deer population size, with decreased use of meadows and forest with increasing red deer numbers, and increased use of areas covered by scree. Ibex habitat use was affected by the population sizes of all three species, but effects differed between species and season. Moreover, horn growth in young chamois and the population growth rate of ibex were negatively related to red deer numbers. The results suggest that high population size of red deer negatively affects ibex and chamois through the migratory behavior of red deer between protected and non-protected areas. Effective management of a migratory ungulate species outside the protected part of its range, taking account of its ecology and natural behavior, can thus have positive effects on populations within a protected area by alleviating interspecific competition. However, this requires co-operation between policy makers and hunters, acceptance by local people, as well as flexibility to deviate from traditional management regimes such as supplementary feeding to tie animals to certain areas.

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INTRODUCTION

Protected areas are often seen as unaffected islands of high conservation value in human-dominated landscapes. However, through borderless ecological processes (Bauer and Hoye 2014), management measures outside protected areas can influence organisms that are resident within them. For instance, a species that performs seasonal migrations between protected areas and areas where it is harvested may compete with resident protected species. The level of interspecific competition will be influenced by management strategies outside the protected area which affect the abundance of individuals migrating into the protected zone. This can result in unexpected effects on populations of conservation concern. Managers and conservationists therefore need better knowledge about ecological processes that occur between protected and non-protected areas.

World-wide, many populations of ungulates have increased in recent decades and are subject to extensive management (Côté et al. 2004), but at the same time, several ungulate populations are at risk of extinction, e.g., due to poaching, habitat fragmentation and isolation (Apollonio et al. 2010). Many populations have restricted ranges and are found within protected areas which are often designed to preserve biotic and abiotic factors and processes to sustain viable populations of the focal species. However, processes which take place over larger scales are often not accounted for. For example, ungulate movement patterns range from resident to nomadic to long-distance migrations, and variation in movement strategy also occurs within species and populations (Milner-Gulland et al. 2011). The spatial scale of migration is in many cases not feasible to include in landscape conservation strategies. If a managed species migrates between protected and unprotected areas, it can potentially impact other species in the protected part of its range. Possible effects include changes in interspecific competition, but also changes in prey availability for predators or alterations in plant communities (e.g., Milner-Gulland et al. 2011, Henden et al. 2014).

Interspecific interactions between ungulates have been shown to range from facilitation (Sinclair and Norton-Griffiths 1982, Gordon

1988, Arsenault and Owen-Smith 2002) to competitive exclusion (Harmel 1980, 1992, Forsyth and Hickling 1998), and can vary within a system depending on animal densities or season (Hobbs et al. 1996, Odadi et al. 2011). For interspecific competition to occur, different species must overlap in habitat use and diet, and the shared resources must be limiting (e.g., de Boer and Prins 1990). Body condition, survival and reproduction in temperate ungulates are often related to foraging conditions during summer, when food is abundant but can vary considerably in quality (White 1983, Festa-Bianchet et al. 1997, Côté and Festa-Bianchet 2001, Herfindal et al. 2006, Cook et al. 2013). Interspecific resource competition during summer is therefore expected to negatively affect body condition and vital rates. Strategies to cope with resource competition include diet shifts while remaining in the same area as the competitor (e.g., Landman et al. 2013), a habitat/range shift to areas with less competition (e.g., Loft et al. 1991), and no dietary or habitat response, resulting in a decrease in energy gain (e.g., Homolka et al. 2008).

While the two native cervids of central Europe, red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), have increased considerably over the last decades (Apollonio et al. 2010), several populations of the two native bovids, Alpine chamois (*Rupicapra rupicapra*) and Alpine ibex (*Capra ibex*), are of conservation concern, and are often found in protected areas (Shackleton 1997, Apollonio et al. 2010). The ecological consequences of co-occurrence of these species with contrasting conservation concern is therefore of direct interest to management. In the Swiss National Park, red deer, chamois and ibex co-exist at relatively high abundance, and all three species primarily use alpine and subalpine meadows for foraging during summer (Fig. 1). While ibex and chamois are resident within the park year-round, red deer migrate from their summer ranges (June–October) inside the protected area to wintering ranges (November–May) at lower altitudes in the Upper and Lower Engadine and neighboring Val Müstair (migration distances of ca. 20–30 km), where they are subject to harvesting. This provides an excellent opportunity to address how migration of a managed species with no conservation concern affects unmanaged species within the protected
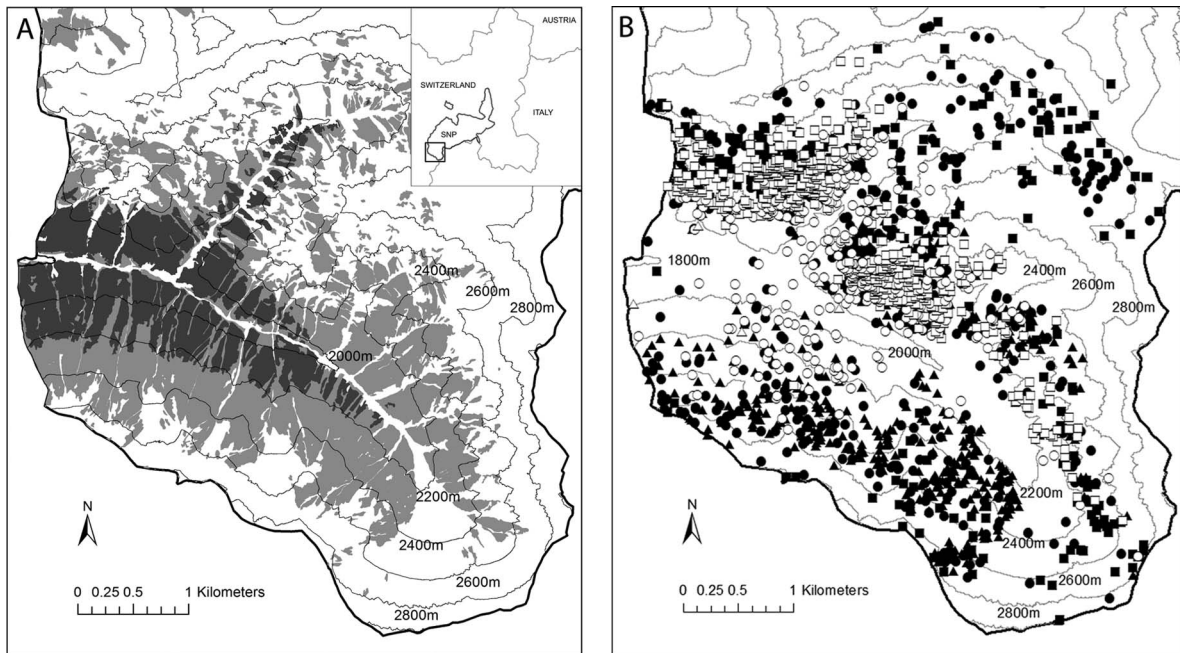
Fig. 1. Location of study area within the Swiss National Park (SNP) with (A) distribution of vegetation types: conifer forest dominated by larch (*Larix decidua* Mill.), Swiss stone pine (*Pinus cembra* L.) and Norway spruce (*Picea abies* (L.) H. Karst; dark gray), alpine and subalpine meadows (light gray) and non-vegetated ground (rock, scree and snow; white), and (B) sighting distributions of chamois (circles), ibex (squares) and red deer groups (triangles) in Val Trupchun during August (filled symbols) and January (open symbols) from 1997 to 2013.

area.

Red deer, ibex and chamois are classed as mixed feeders (i.e., with a diet consisting of both grass and browse; Hofmann 1989). All three species consume to a large extent graminoids, with herbs, sedges and woody plants taken in different proportions depending on area and season (Schröder and Schröder 1984, Klansek et al. 1995, Gebert and Verheyden-Tixier 2001, Bertolino et al. 2009). However, the diet of chamois is generally closer to that of a browser, while the diet of ibex tends to be closer to that of a grazer (Gordon and Illius 1988, Hofmann 1989, Pérez-Barbería et al. 2001). Ibex are often confined to alpine habitats above the tree-line, whereas chamois tend to occupy ranges at intermediate to high altitudes, although both species are found at lower altitudes during winter (Nievergelt 1966, Baumann et al. 2005). Red deer occur in the widest range of habitats from sea level to mountain areas, particularly during summer (Staines and Welch 1984, Welch et al. 1990, Haller 2002). Due to their similar

feeding modes (Hofmann 1989), an overlap in the dietary niches leading to competitive interactions can be expected between these ungulates (see also e.g., Schröder and Schröder 1984, Bertolino et al. 2009).

Firstly, we explored the potential for interspecific competition between red deer, and chamois and ibex, in the Swiss National Park through assessing dietary overlap. Then we investigated how red deer abundance affected ibex and chamois with respect to habitat use, and ultimately body condition and population dynamics. We predicted a shift in habitat use by chamois and/or ibex with increasing red deer numbers during summer if competition played a role. Since horn growth in many young bovids is an indicator of body condition and thus resource availability (Côté et al. 1998, Giacometti et al. 2002, Festa-Bianchet et al. 2004, Rughetti and Festa-Bianchet 2011, Chirichella et al. 2013, Büntgen et al. 2014), we further expected that horn growth in juvenile chamois and ibex would be negatively correlated with red deer popula-

tion size if interspecific competition was enforced through high numbers of red deer migrating into the park. If red deer abundance affected body condition, we predicted a delayed effect of red deer numbers on the population dynamics of ibex and chamois.

MATERIALS AND METHODS

Study area

The study area was located in Val Trupchun, a valley in the south of the Swiss National Park in the central Alps (46.66° N, 10.2° E; Fig. 1). The area covers approximately 22 km^2 at altitudes of 1800–2800 m a.s.l. and is characterized by a continental climate. Based on data recorded at the park's weather station Buffalora (1968 m a.s.l., at a distance of ca. 13 km from Val Trupchun) over the study period (1990–2013), temperatures ranged from an average annual minimum of −28.6 ± 2.4°C (mean ± SD) to an average annual maximum of 24.7 ± 1.2°C with an annual mean of 1 ± 0.5°C. Precipitation was highest in summer and lowest during winter, with annual amounts ranging from 558 mm to 1088 mm, and a yearly average of 831 ± 150 mm (MeteoSwiss 2015). Permanent snow cover lasts from early November to mid-April. The habitat consists predominantly of scree and rocks, alpine and subalpine grassland, and coniferous forest (Fig. 1A; Zoller 1995). The growing season lasts from mid-May until mid-September.

Ungulate numbers in Val Trupchun during summer have fluctuated between 90–201 chamois, 200–408 ibex and 339–635 red deer since 1990 (Fig. 2). Roe deer are only present in low numbers (<3% of the total ungulate population) and were therefore excluded from the analysis. Large mammalian predators are absent from the park. There is no hunting within the boundaries of the Swiss National Park, and animals are further protected from disturbance by visitors being strictly prohibited from leaving the footpaths or bringing dogs into the park.

While there has been no gap in the presence of chamois in the Swiss National Park, ibex had been extinct in Switzerland by the 18th century. Re-introductions started in 1920, and the species re-colonized the study area in Val Trupchun from ca. 1940 onwards (Nievergelt 1966). Red deer were also virtually extinct in eastern Switzerland and surrounding areas in the 17th century, but recolonized the region naturally in the early 20th century, reaching maximum population size in the 1970s (Haller 2002). While chamois and ibex remain within the study area or in its vicinity year-round, most red deer leave the valley after the rut in October/November to wintering areas at lower altitudes, where they are subjected to a targeted culling programme. This area-based management scheme is strictly regulated and involves only few hunters, with quotas dependent on summer censuses and number of adults of each gender taken during the 3-week traditional hunt in September. Since this 2-phase management scheme was introduced in 1987, the total number of red deer taken around the National Park has typically varied between ca. 500 and 650 individuals annually (up to 900 in the first four years), with the culling programme accounting for 42% of individuals shot on average (Amt für Jagd und Fischerei Graubünden; Jenny 2013, Jenny and Filli 2014). This has kept the number of red deer summering within our study area relatively stable with few exceptions confined to more recent years (Fig. 2). Summer population size of red deer within the park is thus directly influenced by humans, while chamois and ibex numbers are not.

Population censuses

Annual censuses of ungulate population sizes have been conducted at maximum seasonal densities of each species (ibex in April; chamois and red deer during July/August) by experienced park rangers since 1990. Counts were conducted from the same fixed points as the spatial distributions were mapped (Haller 2006, 2011; see *Habitat use*). To standardize surveys, they were carried out within a window of two weeks each year on days with optimal viewing conditions. The study area was sub-divided into five separate blocks which could be viewed from the fixed observation points. Double-counting of animals close to the boundaries of adjacent blocks was avoided by noting the time of the sightings, their exact locations and group compositions, and subsequent comparison of these notes between rangers immediately after the surveys (see also Sæther et al. 2002).

Fig. 2. Annual census counts of chamois, ibex and red deer in Val Trupchun 1990–2013.

Diet data and analysis

The potential for interspecific competition was assessed based on dietary overlap between the three species. Fresh fecal samples were collected on February 12th (winter), May 22nd (spring), August 20th (summer) and November 18th (autumn) 2008 by walking 10 m wide transects from the valley bottom up the mountain slope in areas within Val Trupchun where all species had been observed. Twenty chamois and ibex samples (defined as pellet groups separated by a minimum distance of 10 m), and as many red deer samples as possible ($9 \leq n \leq 12$), were collected per season. No red deer samples were found in November.

All samples were frozen at $-20°C$ until processing in an autoclave. The autoclaved samples were then ground in a mortar, 2.5 g of each sample were covered with distilled water, mixed with a blender and rinsed through a sieve (mesh width 0.1 mm). The residue was first washed with water and then with 70% ethanol. All processed samples were stored in 70% ethanol. To identify and count the plant fragments in each sample, the ethanol mixture was placed into a petri dish and allowed to settle for 15 min. A random drop of each sample was transferred onto a microscope slide with a pipette and viewed at a magnification of 200×. Ten epidermal fragments with a minimum area of 0.02 mm^2 were identified to species, genus or plant group level along two transects, starting at the top left corner of each slide. This procedure was repeated 10 times for each sample, resulting in 100 identified plant fragments per sample (Suter et al. 2004, Trutmann 2009, Zingg 2009).

Plant species identified in the fecal samples were grouped into Cyperaceae, Poaceae, herbs, dwarf shrubs (Ericaceae), coniferous trees, ferns and mosses, and unidentified plant parts. For further analysis, ferns and mosses (mean occurrence of $\leq 2.3\%$ per group per season) and unidentified plant parts ($\leq 1.9\%$; see Appendix: Fig. A1) were excluded. The frequencies of each plant group found per sample were square-root transformed and included in a correspondence analysis (CA). A univariate ANOVA, followed by Tukey's post hoc test, was then conducted on the first and second axis scores of the CA, using the species-season combinations as explanatory variable.

Habitat use

In order to assess if red deer displaced chamois and ibex at increasing densities, we examined the habitat use of chamois and ibex and related it to red deer numbers over a 17-year period. The spatial distribution of chamois ($n_{total} = 1967$ individuals in 520 groups in summer; 1158 individuals in 333 groups in winter), ibex ($n_{total} = 941$ individuals in 230 groups in summer; 2142

individuals in 445 groups in winter) and red deer (n_{total} = 6626 individuals in 412 groups in summer; 12 individuals in six groups in winter) in Val Trupchun was mapped by park rangers during one morning in the first half of January and August each year between 1997 and 2013. The exact date depended on when surveys could be conducted safely (i.e., no risk of avalanches) and in good viewing conditions. The study area was divided into five adjacent sub-areas, which were separated based on the optimal viewshed from each observation point. Each ranger record-ed the locations (average accuracy = 30 m; Haller 2006), size and composition of all ungulate groups (distance between individuals ≤100 m) within each sub-area (rotated between rangers on a regular basis) on a printed map at a resolution of 1:25,000 (http://www.swisstopo.admin.ch). All observations were carried out from fixed points overlooking the opposite slope of the valley, so that animals remained undisturbed during the surveys.

Differences in animal group sizes were ac-counted for by multiplying each sighting record with its associated environmental variables by the number of adult individuals in the group. Each observation was assigned the following environmental variables:

- Altitude (m): based on a digital elevation model (DEM) of 4 × 4 m resolution (Haller 2011).
- Slope (degrees): based on the same 4 × 4 m DEM as above and calculated with the Surface tool of the Spatial Analyst Extension in ArcGIS (ESRI 2012).
- Solar radiation: based on the 4 × 4 m DEM and calculated as Area Solar Radiation at 10 am local time on 7th January and 7th August, respectively. Solar radiation was used instead of aspect, as it was considered more relevant in shaping the animals' distribution than aspect alone.
- Terrain ruggedness: calculated after Sap-pington et al. (2007). Each cell of the DEM was assigned a ruggedness value based on the variation in slope and aspect of its neighboring 9 × 9 cells.
- Habitat type: forest, meadow, rock, scree and other non-vegetated ground (e.g., snow, rock glaciers, etc.) based on digital photogram-

metry of near infrared aerial images (Lotz 2006).

All spatial analyses were performed within ArcGIS Version 10.1 (ESRI 2012), with distance units set to metres. Altitude and ruggedness were log-transformed before further analysis in order to meet the requirement of normality. We used the concept of Ecological Niche Factor Analysis (Calenge and Basille 2008) within the adehabitatHS package (Calenge 2006) in R (R Core Team 2013) to combine a factorial compo-sition of the habitat variables of all chamois and ibex observations into environmental axes. We retained the first three axes which all had eigenvalues > 1 to represent the environmental dimensions that were utilized by chamois and ibex over the study period. We then tested for differences in scores along these three axes between summer and winter, and between the two species, to assess overall patterns in habitat use among ibex and chamois. Next, we added numbers of red deer, chamois and ibex to assess how abundance of potentially competing species, as well as intraspecific density effects, influenced a species' habitat use in a given year. We also included interactions between abundance mea-sures and species (chamois or ibex) to investigate species-specific responses in habitat use to abundance, and abundance measures and sea-son, to examine whether abundances were more important for habitat use during winter or summer. Finally, the global model also included three-way interactions between species, season and abundances. A significant relationship be-tween red deer numbers and scores on one of the three axes would indicate that red deer popula-tion size affected the habitat use of chamois or ibex. As red deer are absent from the Swiss National Park during winter but their density during the previous summer might have longer lasting effects through the year, the red deer number from the survey during the previous August was also assigned to winter surveys.

Next we investigated how habitat use was related to the abundance of the migratory red deer and the resident species for the variables that mostly contributed to the variation along the first three axes, which included altitude, radia-tion and habitat type (Table 1). The fixed structure of the models was similar to the

Table 1. Squared correlation coefficients (r^2, for continuous variables), correlation ratio (cr; for habitat) and axis scores along the first three axes of the ordination for chamois and ibex.

	Axis 1		Axis 2		Axis 3	
Variable	r^2/cr	score	r^2/cr	score	r^2/cr	score
Radiation	0.643	−0.608	0.010	0.084	0.011	0.104
Altitude	0.606	−0.591	0.154	−0.334	0.003	0.056
Slope	0.297	0.414	0.173	−0.354	0.156	0.382
Ruggedness	0.075	0.208	0.270	−0.442	0.200	−0.432
Habitat	0.116	…	0.774	…	0.698	…
Forest	…	1.234	…	1.766	…	−0.378
Meadow	…	−0.022	…	0.411	…	0.361
Rock	…	0.084	…	−1.981	…	2.044
Scree	…	−0.126	…	−0.505	…	−0.946

component axis models, whereas the dependent variables were either altitude (ln-transformed) or radiation with a gaussian error structure, or whether observations were in a specific habitat type or not, modeled separately for each habitat type and with a binomial error structure. All habitat models were run as (generalized) linear mixed models ((G)LMM; Bolker et al. 2009) with year as a random factor to account for interdependence in observations within years. Model selection was based on Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002).

Horn growth

Potential negative effects of red deer on the body condition of chamois and ibex were examined by comparing their horn growth with red deer numbers. The Swiss National Park holds a collection of ibex and chamois skulls found within the park that are catalogued and have been measured according to standard protocols (Nievergelt 1966, Schröder and von Elsner-Schack 1985). Annual growth sections of ibex and chamois horns were measured along the posterior end of the horns using a tape measure, and recorded along with associated metadata (location, date, sex and age of animal).

We used horn measurements of all chamois ($n_{males} = 26$, $n_{females} = 29$) and male ibex ($n = 44$) born in 1990 or later, which were found within the study area and were in sufficiently good condition that the year of death could be determined. Female ibex were excluded from the analysis since year rings are not sufficiently conspicuous in their horns. For male ibex, horn growth during the yearling year was measured

as the average length of the yearling sections between left and right sides. Yearling horn growth in year t was compared against population sizes of ibex, chamois and red deer in year t. For chamois, measurements were combined for the kid and yearling sections of the horns due to difficulties in separating these sections in this species. This measure, which includes growth in year t − 1 and t, was compared against the average population sizes of ibex, chamois and red deer of years t − 1 and t. For chamois horn growth, we also included sex as a covariate together with its interaction with population sizes of the three species. Models were fitted as multiple linear regression models and AIC_c was used to assess which variable(s) best explained variation in horn growth, where model selection was run separately for ibex and chamois.

Population growth rates

As a final step to investigate interspecific interactions between the three species, we constructed models of population growth for ibex and chamois, corrected for climatic variation between years (summer precipitation and winter harshness). The amount of rainfall (mm) during the previous growing season (mid-May to mid-September) as a measure for feeding conditions and total winter snowfall (mm; November to mid-April) as a measure for winter harshness were calculated from climate data recorded at the park's weather station Buffalora over the study period (MeteoSwiss 2015) and included as covariates in the models. Results from these analyses did not depend on whether population models were on the arithmetic or log-linear scale, and we therefore chose the arithmetic scale.

Population growth for chamois and ibex was expressed as $\lambda_{t+1} = N_{t+1}/N_t$, and we fitted the following models for chamois and ibex separately:

$$\lambda_{\text{Chamois},t+1} = N_{\text{Chamois},t} + N_{\text{Ibex},t} + N_{\text{Reddeer},t}$$
$$+ \text{ summer precipitation}_{t-1} + \text{winter snowfall}_t$$

and

$$\lambda_{\text{Ibex},t+1} = N_{\text{Ibex},t} + N_{\text{Chamois},t} + N_{\text{Reddeer},t}$$
$$+ \text{ summer precipitation}_{t-1} + \text{winter snowfall}_t$$

where a negative effect of $N_{\text{Chamois},t}$ in the first model or $N_{\text{Ibex},t}$ in the second model suggest intraspecific density dependence, and a negative effect of the other population sizes suggest a negative effect of the abundance of that species on the population growth of the focal species (i.e., ibex or chamois). Models were fitted as linear models and AIC_c was used to evaluate the importance of the variables in describing lambda.

RESULTS

Diet

For all three ungulates, Poaceae had a high frequency of occurrence in the diet year-round (data on red deer diet were not available for autumn). During winter, conifer tree fragments were equally frequent as Poaceae for red deer, while Cyperaceae made up approximately the same proportion in the diet of chamois (Fig. 3). As expected from their seasonal availability, the proportion of herbs in the diet was highest during summer for all three species, while proportions of both Cyperaceae and conifers were more frequent during winter and spring (Fig. 3).

After Bonferroni correction, the first axis of the CA successfully separated the diet of red deer during winter from that of all other species-season combinations (Fig. 3F), resulting from the high proportion of conifer fragments consumed by red deer in winter (Fig. 3E). However, overall separation was relatively poor, and despite a significant seasonal difference, no difference was found between the diet compositions of the three species during either spring or summer (Fig. 3F). Only during autumn did chamois and ibex show a significant difference in diet composition within the same season due to the higher proportion of Cyperaceae and conifer fragments,

and a lower proportion of herbs taken by ibex in comparison to chamois (Fig. 3A, C, E). Species-season patterns in diet were not significant for scores on the second axis after Bonferroni-correction ($p \geq 0.045$).

Habitat use

The decomposition of values of the habitat variables for all observations of chamois and ibex resulted in three axes with eigenvalue larger than 1 (axis 1: 1.74, axis 2: 1.38, axis 3: 1.07). The first axis was mostly explained by radiation ($r^2 = 0.643$) and altitude ($r^2 = 0.606$), but not habitat type (correlation ratio = 0.116). The next two axes were mainly related to habitat type (correlation ratio: Axis 2 = 0.774, Axis 3 = 0.698; see Table 1 for details). Scores along the first axis differed between chamois and ibex, and between summer and winter, but the difference between chamois and ibex was similar between seasons ($\chi^2 = 0.69$, df = 1, $P = 0.407$). For the other axes, the difference in scores between chamois and ibex varied among seasons (i.e., an interaction between species and season, Axis 2: $\chi^2 = 15.83$, df = 1, $P < 0.001$, Axis 3: $\chi^2 = 10.50$, df = 1, $P < 0.001$).

The AIC_c-based ranking of models explaining the temporal variation in axis scores suggested that the scores along all three axes were related to red deer abundance (Table 2). For Axis 1, this relationship differed between chamois and ibex (Fig. 4A; Appendix: Table A1), but was similar for summer and winter habitat use (one of the three highest ranked models included the interaction between season and red deer abundance; $\Delta AIC_c = 1.97$; Table 2, Fig. 4A). For Axis 2, the relationship differed both between season and species (Table 2), and was positive during summer and negative during winter (Fig. 4B; Appendix: Table A1). For Axis 3, there was a negative relationship between the axis value and red deer abundance, which did not differ among season or species (Table 2). Accordingly, there was a negative relationship between habitat use measured along the third axis and N_{Reddeer} (Fig. 4C; Appendix: Table A1).

We then evaluated the impact of red deer abundance on habitat use with respect to the habitat variables which had the highest correlations with the first three axes: altitude, radiation, and habitat type. Habitat use with respect to solar radiation, and the proportion of observa-
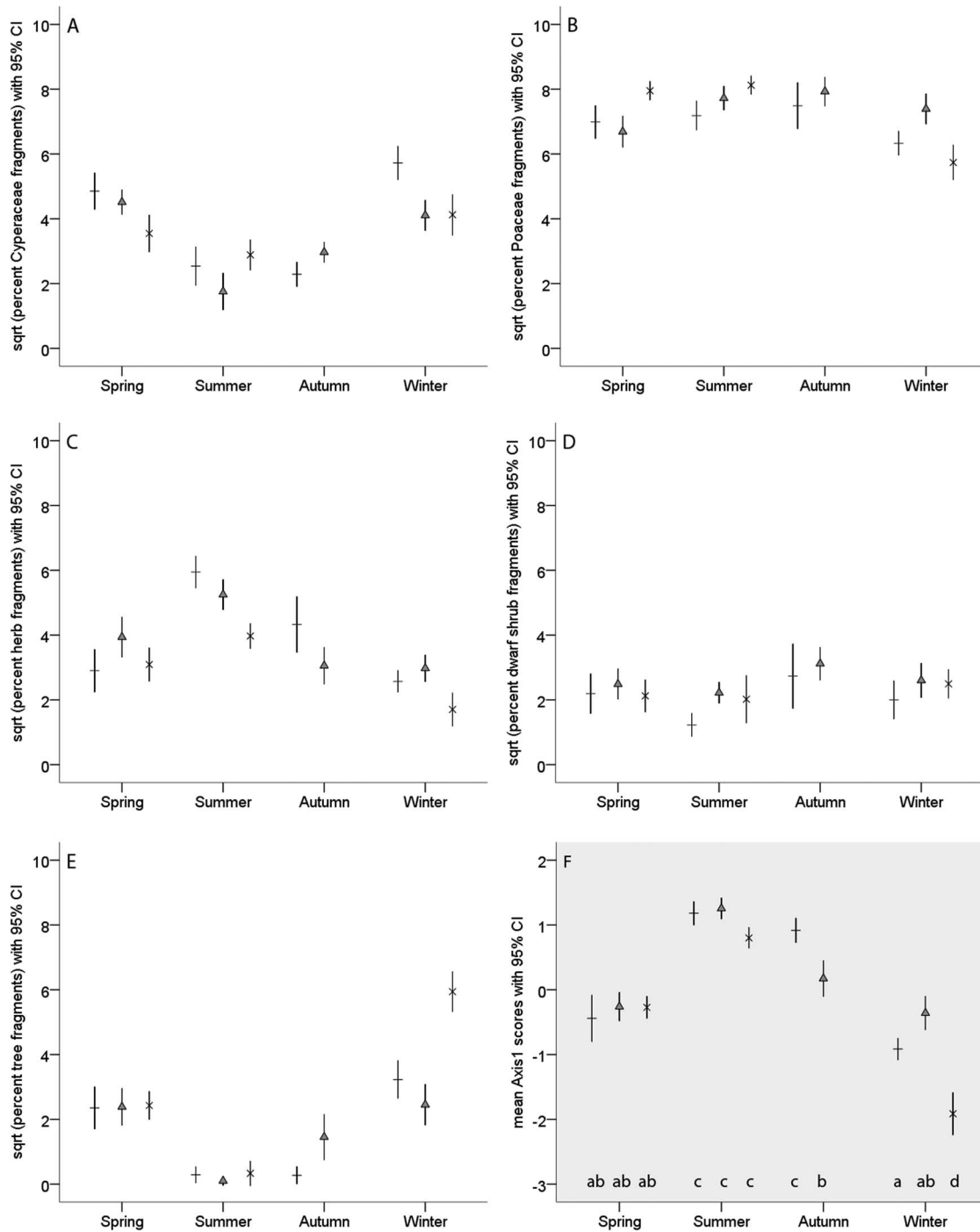
Fig. 3. Mean relative abundance (square-root transformed) ± 95% confidence intervals (CI) of the five most frequently detected plant groups found in fecal pellets of chamois (horizontal bars; $n = 20$ for each season), ibex (gray triangles; $n = 20$ for each season) and red deer (crosses; $n = 12$ for spring and winter, $n = 9$ for summer, no data for autumn). Panel (F) shows the mean first axis scores of the correspondence analysis (CA) for diet composition in chamois, ibex and red deer (same symbols as above). Letters above the x-axis indicate homogeneous groups of species-season combinations according to Tukey's post hoc test.

Table 2. AIC$_c$-based ranking of candidate models explaining chamois and ibex habitat use as described by the first three axes of a component analysis of all habitat variables, during summer and winter in Val Trupchun, Swiss National Park, in relation to abundance of red deer (N_{Rd}), chamois (N_{Ch}) and ibex (N_{Ib}).

Axis	Sp	Se	N_{Rd}	N_{Ch}	N_{Ib}	Sp × Se	Sp × N_{Rd}	Sp × N_{Ch}	Sp × N_{Ib}	Se × N_{Rd}	Se × N_{Ch}	Se × N_{Ib}	Sp × Se × N_{Rd}	Sp × Se × N_{Ch}	Sp × Se × N_{Ib}	ΔAIC$_c$	AIC$_c$ weights
1	X	X	X	X	X	X	X	X	…	…	X	X	…	X	…	0.00	0.37
	X	X	X	X	X	X	X	X	X	…	X	X	…	X	…	1.22	0.20
	X	X	X	X	X	X	X	X	…	X	X	X	…	X	…	1.97	0.14
	X	X	X	X	X	X	X	X	X	…	X	X	…	X	X	2.93	0.09
	X	X	X	X	X	X	X	X	X	X	X	X	…	X	…	3.22	0.07
2	X	X	X	X	X	X	X	…	X	X	X	X	…	…	X	0.00	0.13
	X	X	X	X	X	X	X	X	X	X	X	X	…	X	X	0.69	0.09
	X	X	X	X	…	X	X	…	X	X	…	X	…	…	X	0.75	0.09
	X	X	X	X	X	X	X	…	X	X	X	X	X	…	X	1.58	0.06
	X	X	X	X	X	X	X	X	X	X	X	X	…	…	X	1.87	0.05
3	X	X	X	X	X	X	…	X	…	…	…	…	…	…	…	0.00	0.04
	X	X	X	…	X	X	…	…	…	…	…	…	…	…	…	0.06	0.04
	X	X	X	X	…	X	…	X	…	…	…	…	…	…	…	0.60	0.03
	X	X	X	…	X	X	…	…	…	X	…	…	…	…	…	0.78	0.03
	X	X	X	X	X	X	…	X	…	X	…	…	…	…	…	1.06	0.02

Note: Abbreviations are: Sp, species; Se, season.

tions in rocky habitat, was not related to red deer abundance (Table 3). The altitudinal distribution of ibex and chamois was best explained by abundance of red deer and its interaction with species, but an alternative model with $\Delta AIC_c = 0.68$ did not include $N_{Reddeer}$ (Table 3). Indeed, the altitudinal distribution of chamois was not related to $N_{Reddeer}$ (Fig. 4D; Appendix: Table A1), whereas the altitudinal distribution of ibex was only weakly negatively related to $N_{Reddeer}$ (Fig. 4D, 95% credible intervals overlapped zero; Appendix: Table A1). The proportion of observations in forest was related to $N_{Reddeer}$, and differently between ibex and chamois and during summer and winter (Table 3). For chamois, there were negative relationships between the proportion of observations in forests and red deer abundance for both seasons (Fig. 4F; Appendix: Table A1). For ibex, the relationship was positive during summer and weakly negative during winter (Fig. 4F; Appendix: Table A1). The proportion of observations on meadows was negatively related to $N_{Reddeer}$ in a similar manner for ibex and chamois, both during summer and winter (Fig. 4G; Appendix: Table A1). Finally, the proportion of observations on scree in a given year was differently related to $N_{Reddeer}$ between seasons and species (Table 3). There was a positive relationship between $N_{Reddeer}$ and the proportion of chamois observations on scree during both seasons, whereas for ibex the

relationship was positive during winter and negative during summer (Fig. 4I; Appendix: Table A1).

Habitat use by ibex and chamois was also affected by the abundance of ibex and chamois, suggesting both density-dependent effects on habitat use and that there were interactions between ibex and chamois, in addition to the interaction between red deer and the two resident species (Tables 2 and 3). The overall pattern was that chamois habitat use was affected by N_{Ibex} or $N_{Chamois}$ to a small extent, but strongly affected by $N_{Reddeer}$, whereas ibex habitat use was affected by the abundance of both $N_{Reddeer}$ and $N_{Chamois}$, as well as N_{Ibex}. Details regarding these relationships are found in Appendix: Table A1.

Horn growth

The highest ranked model explaining chamois horn growth during the first two years of life included population size of red deer ($N_{Reddeer,t}$) and sex, with low support for alternative models (all $\Delta AIC_c > 1.90$; Table 4). According to this model, chamois horn growth was negatively related to $N_{Reddeer,t}$ in a similar way for male and female chamois (Fig. 5A). Yearling horn growth in male ibex was, according to AIC$_c$ values, related to $N_{Chamois,t}$ (estimate: 0.019, SE = 0.007), but not related to $N_{Reddeer,t}$ (Fig. 4B) or $N_{Ibex,t}$ (Table 4).
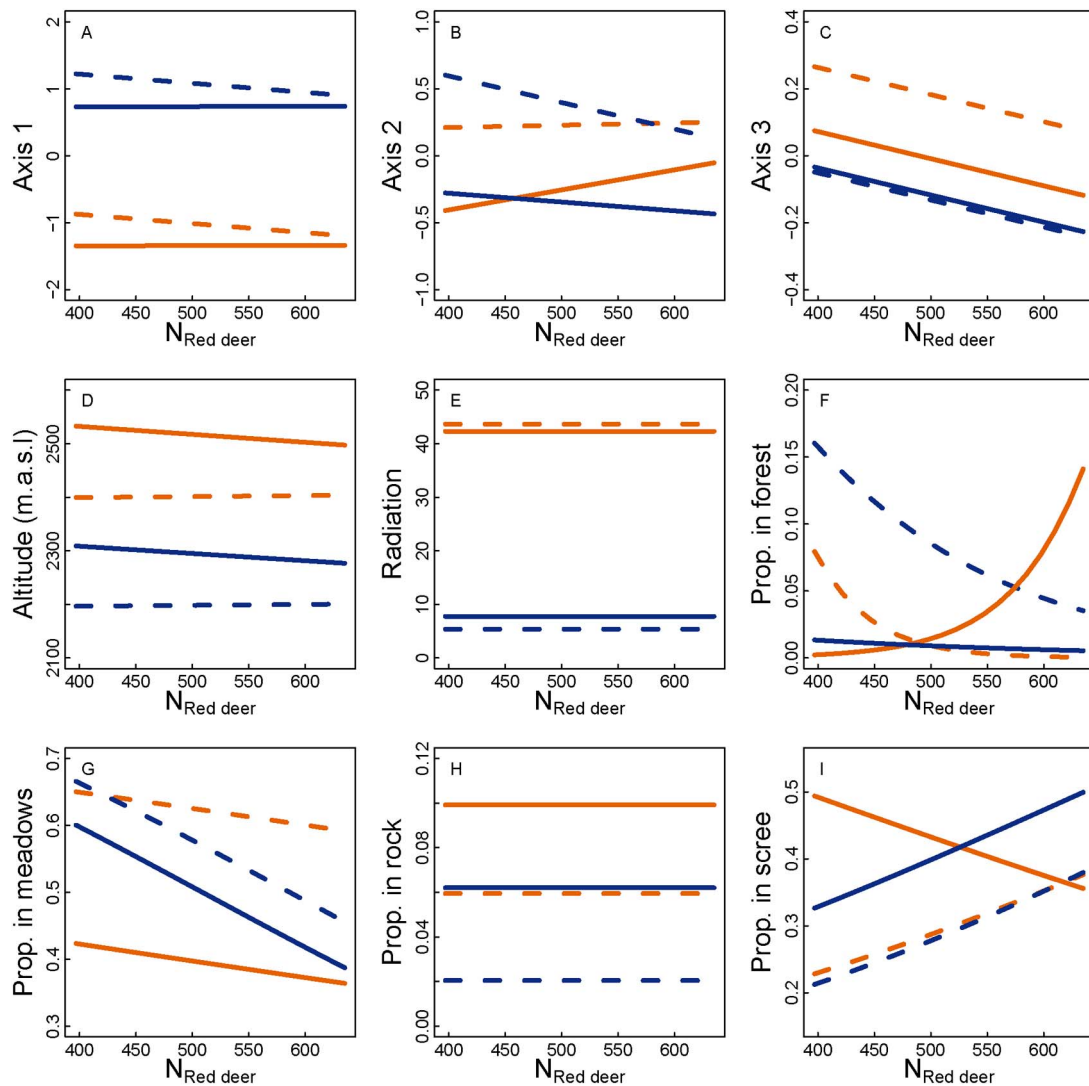
Fig. 4. Relationship between abundance of red deer during summer and habitat use of male and female ibex and chamois described by the first three axes of the habitat decomposition by factorial analysis of the habitat variables (see Table 1 for relationship between axes and habitat variables). Dashed and solid lines are chamois and ibex, respectively, whereas orange and blue represent summer and winter habitat use. Relationships are based on the highest ranked models in Tables 2 and 3. See also Appendix: Table A1 for parameter estimates and 95% credible intervals.

Population growth rates

The AIC_c-based model selection for the growth rate of the chamois population suggested a negative feedback associated with density dependence (estimate of $N_{Chamois,t}$: −0.0055, SE = 0.0015), and a negative relationship with winter harshness (estimate of winter snowfall: −0.0013, SE = 0.0005), but no relationship with red deer population size (Table 5, Fig. 5C). Ibex population growth rate was also density-dependent (estimate of $N_{Ibex,t}$: −0.0011, SE = 0.0004) and was negatively related to $N_{Reddeer,t}$ (estimate of $N_{Reddeer,t}$: −0.0013, SE = 0.0004; Fig. 5D) and winter harshness (estimate of winter snowfall: −0.0005, SE = 0.0003), while it was independent of $N_{Chamois,t}$ (Table 5).

Table 3. AIC$_c$-based ranking of candidate models explaining chamois and ibex habitat use during summer and winter in Val Trupchun, Swiss National Park, in relation to abundance of red deer (N$_{Rd}$), chamois (N$_{Ch}$) and ibex (N$_{Ib}$).

Variable	Sp	Se	N$_{Rd}$	N$_{Ch}$	N$_{Ib}$	Sp × Se	Sp × N$_{Rd}$	Sp × N$_{Ch}$	Sp × N$_{Ib}$	Se × N$_{Rd}$	Se × N$_{Ch}$	Se × N$_{Ib}$	Sp × Se × N$_{Rd}$	Sp × Se × N$_{Ch}$	Sp × Se × N$_{Ib}$	ΔAIC$_c$	AIC$_c$ weights
Altitude	X	X	X	X	X	X	X	X	X	…	X	X	…	X	X	0.00	0.18
	X	X	…	X	X	X	…	X	X	…	X	X	…	X	X	0.68	0.13
	X	X	X	X	X	X	X	X	X	X	X	X	…	X	X	0.81	0.12
	X	X	X	X	X	X	X	X	X	…	X	X	…	X	…	0.92	0.11
	X	X	X	X	X	X	X	X	X	X	X	X	…	X	…	1.58	0.08
Radiation	X	X	…	X	…	X	…	X	…	…	X	…	…	X	…	0.00	0.16
	X	X	…	X	X	X	…	X	…	…	X	X	…	X	…	0.84	0.11
	X	X	…	X	X	X	…	X	…	…	X	…	…	X	…	1.39	0.08
	X	X	X	X	…	X	…	X	…	…	X	…	…	X	…	1.62	0.07
	X	X	…	X	X	X	…	X	X	…	X	X	…	X	…	1.74	0.07
Forest	X	X	X	X	X	X	X	X	X	X	X	X	X	…	X	0.00	0.31
	X	X	X	X	X	X	X	X	X	X	…	X	X	…	X	0.64	0.23
	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	1.60	0.14
	X	X	X	X	X	X	X	…	X	X	X	X	X	…	X	1.74	0.13
	X	X	X	X	X	X	X	…	X	X	…	X	X	…	X	2.37	0.10
Meadow	X	X	X	X	X	X	…	X	X	X	X	X	…	X	…	0.00	0.09
	X	X	X	…	X	X	…	…	X	X	…	X	…	…	…	0.41	0.07
	X	X	X	X	X	X	…	X	X	X	X	X	…	X	X	1.11	0.05
	X	X	X	X	X	X	…	X	X	…	X	X	…	X	…	1.20	0.05
	X	X	X	X	X	X	…	…	X	X	X	X	…	…	…	1.53	0.04
Rock	X	X	…	X	…	X	…	X	…	…	…	…	…	…	…	0.00	0.05
	X	X	…	X	…	X	…	…	…	…	…	…	…	…	…	0.95	0.03
	X	X	…	X	…	X	…	…	…	…	X	…	…	…	…	1.05	0.03
	X	X	…	X	X	X	…	X	…	…	…	X	…	…	…	1.24	0.03
	X	X	…	X	…	X	…	X	…	…	X	…	…	…	…	1.34	0.02
Scree	X	X	X	X	X	X	X	…	X	X	…	X	X	…	…	0.00	0.15
	X	X	X	…	X	X	X	…	X	X	…	X	X	…	…	0.66	0.11
	X	X	X	X	X	X	X	…	X	X	X	X	X	…	…	1.79	0.06
	X	X	X	X	X	X	X	…	X	X	…	X	X	…	X	1.90	0.06
	X	X	X	X	X	X	X	X	X	X	…	X	X	…	…	1.99	0.06

Note: Abbreviations are: Sp, species; Se, season.

DISCUSSION

Impacts of migrants on ecologically similar resident species depend on resource availability, overlap in resource use and animal densities (Bauer and Hoye 2014). In our study system, migratory red deer exceeded chamois numbers between two- and five-fold and occurred at the same to up to 2.5 times the population size of ibex during summer (Fig. 2). Dietary overlap between the three species was high (Fig. 3), suggesting potential for interspecific competition. A negative impact of the migratory species at high population density on the two resident species was suggested by (1) a significant influence of red deer numbers on the use of different habitat types particularly by chamois (Fig. 4, Tables 2, 3; Appendix: Table A1), (2) a negative effect of increasing red deer abundance on horn growth in young chamois (Fig. 5A, Table

4), and (3) a negative effect of increasing red deer abundance on the population growth rate of ibex (Fig. 5D, Table 5). This interspecific competition appeared to have effects of similar or even higher magnitude as some intraspecific density-dependent effects (Tables 2–5; Appendix: Table A1).

Red deer have been shown as superior competitors over several other ungulates. For instance, roe deer respond to red deer by habitat displacement (Danilkin 1996), decreased fawn body mass (Richard et al. 2010), and reduced population sizes (Vladyshevskii 1968, Latham et al. 1996, 1997). Similarly, reintroduced red deer had negative impacts on several individual and population measures of performance on the threatened Apennine chamois (*Rupicapra pyrenaica ornata*) in central Italy (Lovari et al. 2014). Our results are in line with these studies, and together they increase the impression of red deer as a strong competitor over other ungulates.

With increasing red deer abundance, chamois

Table 4. AIC_c-based selection of models explaining variation in horn growth during the first two years of life for chamois (males and females), and during the yearling year for ibex (only males), in relation to population sizes of chamois (N_{Ch}), ibex (N_{Ib}) and red deer (N_{Rd}) during the period of horn growth, and between males and females (chamois only). Only the five highest ranked models are shown.

Response variable	N_{Rd}	N_{Ch}	N_{Ib}	Sex	Sex × N_{Rd}	Sex × N_{Ch}	Sex × N_{Ib}	ΔAIC_c	AIC_c weights
Chamois horn growth	X	…	…	X	…	…	…	0.00	0.35
	X	…	…	X	X	…	…	1.90	0.14
	X	…	X	X	…	…	…	2.37	0.11
	X	X	…	X	…	…	…	2.38	0.11
	X	…	X	X	…	…	X	3.12	0.07
Ibex horn growth	…	X	…	…	…	…	…	0.00	0.53
	…	X	X	…	…	…	…	2.42	0.16
	X	X	…	…	…	…	…	2.42	0.16
	…	…	…	…	…	…	…	4.45	0.06
	…	X	X	…	…	…	…	4.96	0.04

and ibex moved primarily to different habitat types rather than areas of different topography. This effect was stronger for chamois than for ibex and involved a decrease in the use of meadows and forest, coinciding with increased usage of areas covered by scree, where forage density is lower (Fig. 4F, G, I; Appendix: Table A1). Lovari et al. (2014) suggested that trampling on meadows heavily used by red deer played an important role in decreasing grassland quality for Apennine chamois. Results from long-term observation plots and succession models in the Swiss National Park suggest that trampling positively affects 'typical' pasture plants such as red fescue (*Festuca rubra* L.) and quaking-grass (*Briza media* L.). These species are palatable and also relatively disturbance-resistant. At the same time, trampling reduced the abundance of some tall-growing, disturbance-sensitive and unpalatable species such as monk's hood (*Aconitum napellus* L.), which is poisonous (Schütz et al.

2000). On the other hand, selective grazing by red deer favours unpalatable plant species which grow low to the ground, have morphological or chemical defences, or a short life span (Schütz et al. 2003). It is therefore difficult to determine whether the shift in habitat use particularly by chamois was caused by long-term changes in vegetation composition on preferred meadows through trampling or selective foraging by red deer, or by exploitation competition. Both could explain why effects of high summer red deer population size seem to persist into winter. Long-term changes in vegetation composition likely also affect plant groups which chamois and ibex rely on during winter. Exploitation competition would have the effect of short-grass meadows intensively grazed by red deer over the entire growing season being unlikely to contain sufficient nutrients to sustain the resident species later in the year. The shift in habitat use may therefore affect body condition and thus winter survival

Table 5. AIC_c-based selection of models explaining variation in population growth rate ($\lambda_{Ch,t+1}$ and $\lambda_{Ib,t+1}$) in relation to population sizes of chamois ($N_{Ch,t}$), ibex ($N_{Ib,t}$), red deer ($N_{Rd,t}$) and climatic conditions. Only the five highest ranked models are shown.

Response variable	$N_{Rd,t}$	$N_{Ch,t}$	$N_{Ib,t}$	Summer precipitation	Winter snowfall	ΔAIC_c	AIC_c W
$\lambda_{Ch,t+1}$	…	X	…	…	X	0.00	0.33
	…	X	X	…	X	0.94	0.20
	X	X	…	…	X	2.71	0.08
	…	X	X	…	…	2.94	0.08
	…	X	…	…	…	3.02	0.07
$\lambda_{Ib,t+1}$	X	…	X	…	X	0.00	0.31
	X	…	X	…	…	0.63	0.23
	X	…	X	X	X	1.98	0.11
	X	…	X	X	…	2.86	0.07
	X	X	X	…	X	3.71	0.05
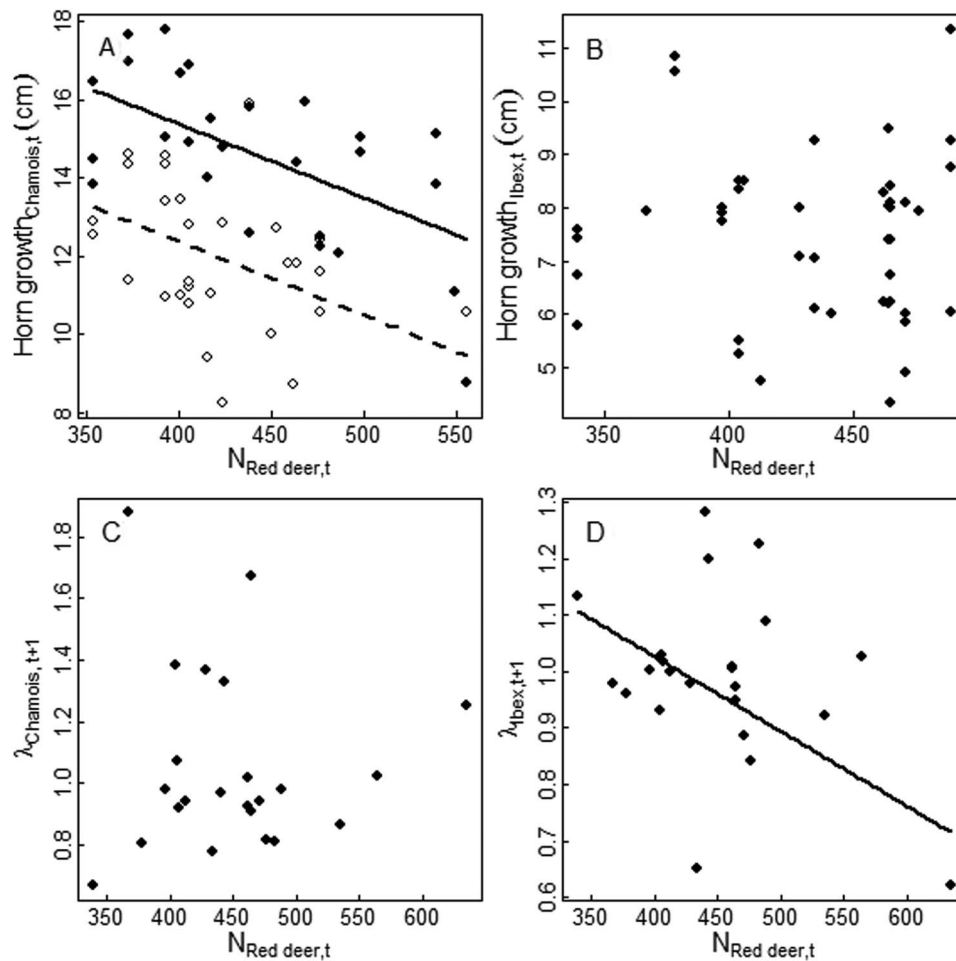
Fig. 5. Relationship between red deer abundance in year t and horn growth in year t of male and female chamois (A), and male ibex (B), and population growth rate from year t to t + 1 (λ_{t+1}), of chamois (C) and ibex (D). In (A), horn growth is measured as the total growth during the kid and yearling years, and $N_{Reddeer,t}$ is calculated as the mean for those two years. Open shapes and the dashed line represent females, and filled shapes and the solid line represent males. Lines indicate that $N_{Reddeer,t}$ was included in the best model, based on AIC_c, explaining variation in the response variable (see Tables 4 and 5).

and/or reproductive success of individuals. However, the effect of increasing red deer summer population size on the two species differed, with a negative influence on the horn growth of chamois, but not ibex. At the same time, the positive correlation between ibex horn growth and chamois population size suggests that the two species are similarly affected by environmental conditions and that chamois do not negatively affect ibex (although they influence ibex habitat use; Appendix: Table A1). This is corroborated by the lack of an effect of chamois population size on ibex population growth rates

(Table 5). Both chamois and ibex population growth rates showed intraspecific density-dependence and a negative relationship with winter snowfall. However, chamois population growth rate appeared more robust to increases in the population size of the migratory competitor than that of ibex. Yet, a negative correlation had been detected between chamois and red deer numbers in the Swiss National Park during the 1970s and 1980s, when red deer were at their maximum population size of over 2000 individuals (Haller 2013).

The migratory behavior of red deer opens the

study system to influences from outside the protected area. In the absence of natural predators, management of the migratory species outside its protected range can alleviate negative effects from interspecific competition on resident species. Wild ungulate population densities are commonly controlled either through regulated recreational hunting (e.g., Bunnell et al. 2002) or targeted culling programmes (e.g., Kilpatrick et al. 1997). A combination of both strategies may in many cases be most beneficial, as it can ensure cost-effectiveness and public acceptance, while at the same time being able to achieve particular aims such as the fulfilment of sex- and age-related quotas and control of local densities. The canton Grison's traditional hunt in September, during which adult males and females without calves are targeted in their summer areas except for animals within the park or other protected areas, is combined with a dedicated area-based culling programme targeting mainly females with calves in November/December, when the animals are in their wintering grounds (Jenny 2013). This 2-stage strategy not only allows for regional adjustment of red deer densities to prevent economic damage in the animals' wintering ranges or winter starvation without supplementary feeding, but permits control of animal numbers summering in the National Park, which are inaccessible to the traditional September hunt. Without the culling programme in winter, negative effects of the migratory species on the two resident species in the park would likely be even more pronounced.

In the absence of natural predators, conservation and economic interests outside protection zones can probably be combined best by a hunting system that takes the ecology and natural behavior of the target species into account. In our local example, this ungulate management strategy outside protected areas not only benefits resident species through reduced competition, but further advantages also include smaller winter aggregations and thus less damage to agricultural land, more natural behavior of the target species within the protected area (e.g., leaving the cover of trees to feed on meadows also during the day) and thus better wildlife viewing opportunities for National Park visitors (Jenny and Filli 2014). However, the success of such a management strategy depends on the surrounding habitat of a protected area. Ideally, the area surrounding a National Park with migratory ungulates should contain a network of quiet zones with migration corridors between them in order to avoid large winter aggregations outside the park boundaries. This is only possible in relatively sparsely inhabited areas, such as in many mountainous regions of the world or on prairies. There also needs to be acceptance of management measures by local people and governments such as tolerance to certain degrees of browsing on federal lands, acceptance of culling mothers and calves, and giving up of supplementary feeding to artificially tie animals to certain areas.

It is expected that the foreseeable re-colonisation of many areas in central and western Europe by mammalian predators will alter competitive interactions between ungulates (e.g., Holt 1984). High red deer densities in protected alpine areas during summer may lead to higher abundance of resident predators than would be sustained by resident chamois and/or ibex alone (see also Seip 1992, Wittmer et al. 2005). The presence of migratory populations of red deer during summer would probably decrease predation pressure on sympatric species temporarily. However, similar to lions and hyenas switching to resident prey species in the Serengeti when migratory ungulates are unavailable (Sinclair 2003), predators such as wolves might switch to resident ibex and/or chamois during times of the year when red deer are located at lower altitudes in closer proximity to humans. Additionally, the presence of mammalian predators will influence distribution patterns and behavior of their prey, which will in turn require adjustments in management.

Acknowledgments

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Supplemental Material

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