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Resource competition between chamois, alpine ibex and red deer in the Swiss National Park?

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Abstract

Protected areas provide unique opportunities to investigate species interactions under natural conditions. In the absence of large predators, ungulates have reached relatively high densities in the Swiss National Park, and in some valleys, chamois, alpine ibex and red deer co-occur in close proximity. We explored the potential for resource competition between the three species by integrating information on local diet composition and fine-scale spatial distribution with respect to environmental parameters in the valley with the highest ungulate density in the Park. We then tested for correlations in a) their respective population sizes from census data collected over the last 21 years, and b) correlations between census sizes and body condition of chamois and ibex, measured as yearling horn growth.

Based on a correspondence analysis, no difference was detected in diet composition between the three species during spring and summer. Chamois and ibex showed significantly different diets only in autumn, and red deer in winter, although diet composition varied seasonally for all three species. The discrimination success between chamois and ibex based on environmental parameters was also poor, but both species could be differentiated well from red deer. An intermediate negative correlation was detected between the census sizes of red deer in year n and that of ibex in year n+1, while population sizes within the same year were not correlated. Horn growth of young chamois was negatively correlated with the number of red deer in the Park during summer. It is thus likely that local resource competition with red deer has a negative influence on ibex population size with a lag effect of one year (possibly linked to body condition over winter), and on chamois body condition.

Keywords

niche differentiation, alpine ungulate, habitat use, diet, horn growth

Introduction

In the absence of natural predators, ungulate populations in some protected areas in Europe have reached high densities, potentially leading to increases in intra- and interspecific competition. The latter is often difficult to demonstrate in mobile wild populations without removal experiments, which is not possible within protected areas. An integrated approach comparing measures of niche differentiation with evidence for inverse population trends or changes in body condition in sympatry is therefore necessary. Here we investigated both niche differentiation (diet and habitat use) and evidence for competition (population trends and body condition based on yearling horn growth in bovids) between chamois, ibex and red deer in a valley with high densities of all three species within the Swiss National Park.

Methods

Niche differentiation:

- **Diet**: based on dung samples collected in February, May, August and November in 2008. Plants found in samples were grouped into Cyperaceae, Poaceae, herbs, Ericaceae and conifer fragments. A correspondence analysis was then conducted on the frequency of each group per sample, followed by Anova.
- **Habitat use**: based on regular mapping of the spatial distribution of ungulates during one morning in January, May, August and November 1997 to 2012. The analysis was based on the following environmental parameters: altitude, slope, aspect, topographic roughness, percentage of area covered by meadow and rock, respectively, within a 50m radius of each animal. The data were analysed using Generalised Additive Mixed Models (GAMMs) with a binomial distribution for each species pair.

Evidence for competition:

- **Population trends:** based on yearly ungulate censuses 1990 - 2011. Spearman correlations were conducted between the logarithm of population changes for each species pair.

- **Body condition:** based on horn growth of male yearling ibex and male and female chamois kids and yearlings born in 1990 or later. Spearman correlations were conducted between the horn growth and census sizes of all three species in corresponding years.

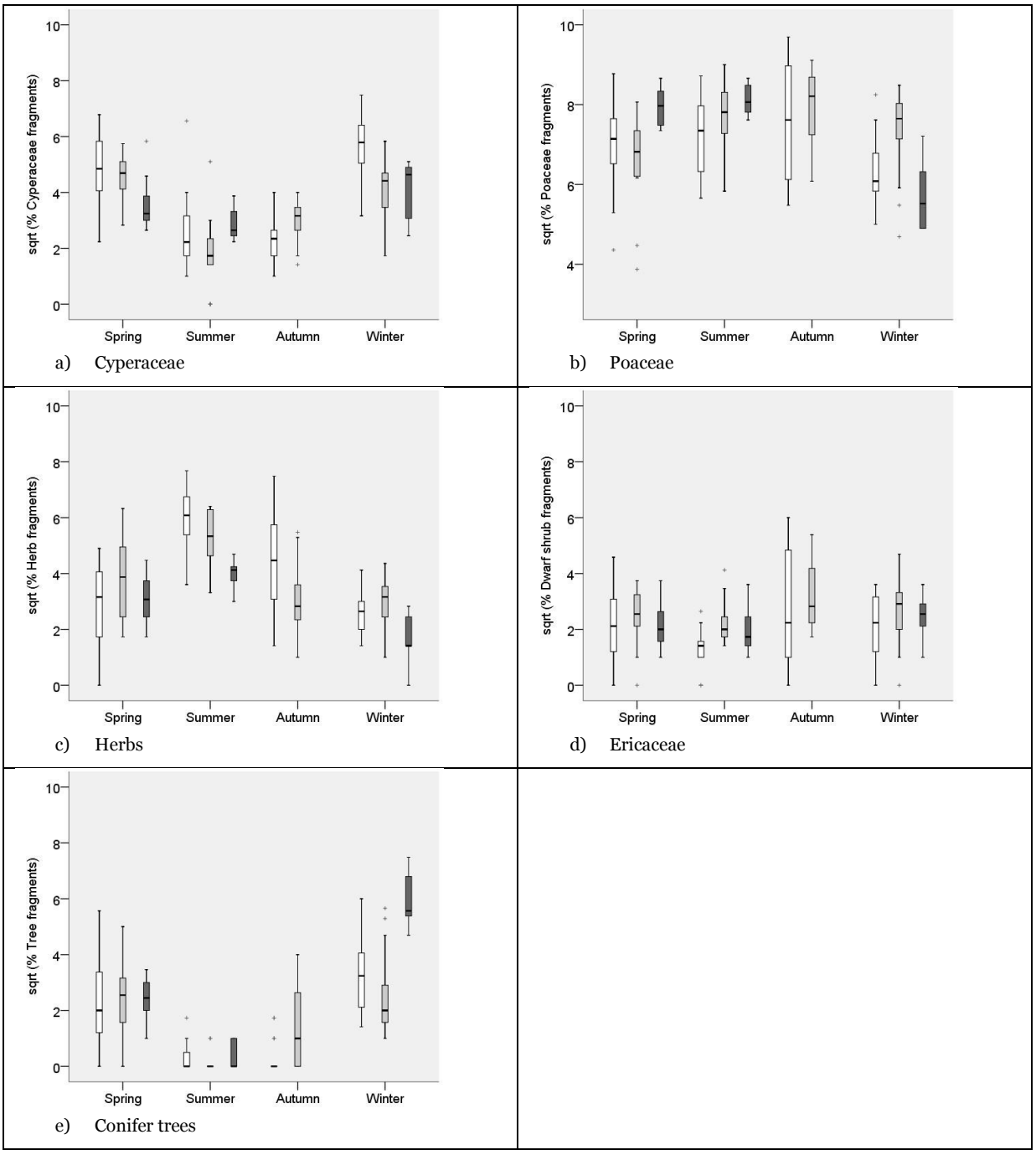

Figure 1: Boxplots for relative abundance (square-root transformed) of the five most frequently represented plant groups found in fecal pellets of chamois (white bars; n=20 for each season), alpine ibex (light grey bars; n=20 for each season) and red deer (dark grey bars; n=12 for spring and winter, n=9 for summer, no data for autumn) in the study area (Val Trupchun). Horizontal bars represent the median, box heights the interquartile range, and whiskers span 1.5 x interquartile range. Outliers (>1.5 x interquartile range) are denoted by +.

Results

Niche differentiation:

Diet: Overall, the variation in the proportion of different plant groups in the diet of chamois, ibex and red deer was higher for the same species between seasons than between species within the same season (Figure 1). There was no difference in diet composition between the three species during either spring or summer, only between chamois and ibex during autumn, and between red deer and the two bovids in winter.

Habitat use: Habitat segregation was weak between chamois and ibex during all seasons. However, the habitat use of red deer differed from the other two species during summer (distributional data for red deer were not available for the other seasons, since the species only occurs within the National Park during summer).

Competition:

Population trends: An intermediate negative correlation was detected between the change in census size of red deer from year t to t+1 vs. the census size of alpine ibex from year t+1 to t+2 (Spearman's rho = -0.58, p = 0.007). However, no negative relationship was found between the changes in counts of red deer from year t to t+1 to that of chamois the following year, nor between chamois vs. ibex or ibex vs. chamois (Spearman's rho < |0.3|, p > 0.2; Figure 2).

Body condition: Horn growth of male chamois during their kid and yearling years combined showed a significant intermediate positive correlation with the average overall number of ibex over the same time period (Spearman's rho = 0.66, p = 0.001), but a negative correlation with the average total number of red deer (Spearman's rho = -0.601, p = 0.004). The horn growth of female chamois during their kid and yearling years combined was significantly negatively correlated only with the average number of male red deer (Spearman's rho = -0.643, p < 0.001). On the other hand, horn growth in yearling male ibex was not correlated with the census sizes of any of the three species during the same year ($0.020 \leq |r| \leq 0.157$; $p \geq 0.376$).

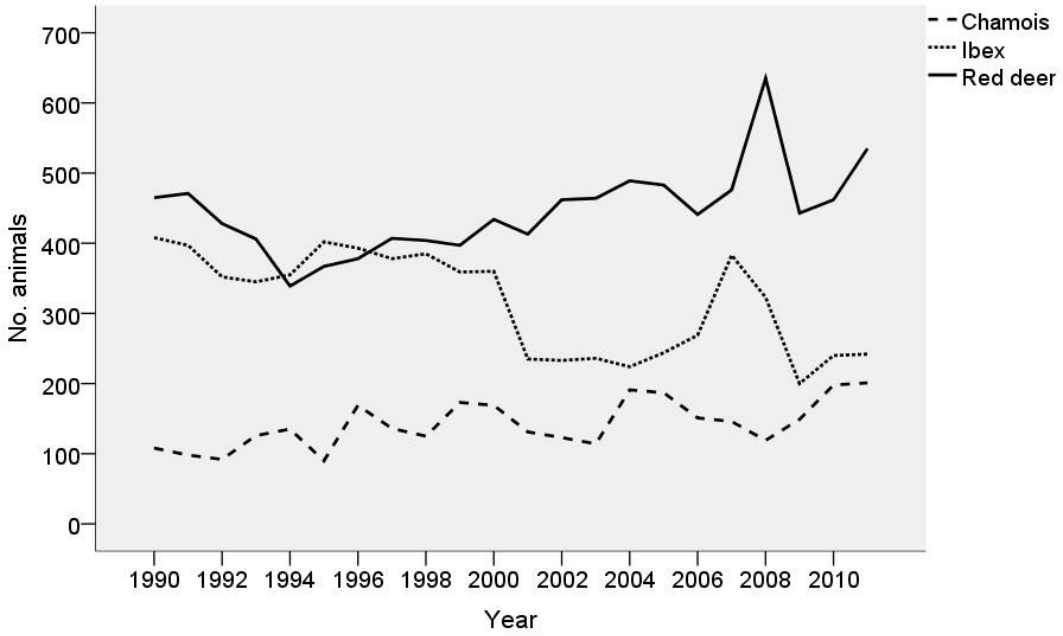

Figure 2: Annual census counts for red deer, chamois and alpine ibex in the study area (Val Trupchun) 1990-2011.

Discussion

The high niche overlap between chamois and ibex with respect to both diet and habitat use could be interpreted as high potential for competition (e.g. BELOVSKI 1986; JENKINS & WRIGHT 1988). However, we found no evidence for competition between chamois and ibex either with respect to reverse trends in population sizes between 1990 and 2011, or the density of one species negatively influencing body condition (i.e. horn growth) of the other. By contrast, there was a significant positive relationship between the horn growth of young male chamois and the total population size of ibex, suggesting that body condition, survival and fecundity of the two species are determined more by common environmental factors than by competitive interactions, at least at their current population densities.

On the other hand, niche differentiation between red deer and both bovid species was high with respect to habitat use (though not with respect to diet) during summer. Combined with the fact that red deer are absent from the Park during winter and only co-occur with chamois and ibex in significant numbers during a time when resources are expected to be abundant, little or no competition would be expected between red deer and chamois, or red deer and ibex. However, a significant negative correlation was found between the changes in census size of red deer and ibex with a time lag of one year, and the horn growth of young male and female chamois was also negatively correlated with the census size of red deer. At the same time, there was no evidence for any effect of intraspecific competition on horn growth. High numbers of red deer thus seem to have a negative influence on both ibex and chamois, although the effect appears to be different for the two species.

Conclusions

In accordance with LISTER (1980) and PIANKA (1980), our results confirm that high niche overlap between species does not necessarily imply the existence of competition, and vice versa, that interspecific competition cannot be ruled out based on a high degree of niche differentiation during a time when resources are abundant.

Natural interruptions of population growth in chamois and ibex by high mortality during harsh winters (e.g. GRØTAN et al. 2008) may keep populations of both species below levels at which resources become limiting and thus enable their coexistence in the same area with little interspecific competition.

It is likely that the foreseeable natural re-colonisation of the Swiss Alps by predators will alter competitive interactions between chamois, ibex and red deer.

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