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Feeding ecology of alpine chamois living in sympatry with other ruminant species

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The populations of Alpine chamois *Rupicapra rupicapra rupicapra* are currently not at risk of extinction, but local population declines have been observed in some areas. Competition with other herbivore species may be one of the causes for this decline. The present research aims at describing the autumnal diet and preferences of Alpine chamois living in sympatry with red deer *Cervus elaphus* and roe deer *Capreolus capreolus* in central Italian Alps and to verify the presence of spatial and diet overlap among these herbivore species. We analyzed the rumen content of 35 samples collected during the hunting season from animals culled in Val Fontana. The results were integrated by data previously collected on rumen content of red deer and roe deer and on space use of the three herbivore species in the same study area. We identified 26 species and 15 genera belonging to 21 plant families of the 51 available in the study area. Monocotyledon families were the most frequently represented in chamois diet composition (78.11%), followed by Ericaceae (5.30%), Betulaceae (4.32%) and Cupressaceae (3.37%). All results showed similar diet between genders. Chamois diet was more similar to red deer than to roe deer diet. The diet selection index (W_m) showed that on the east-facing side of the valley some species (*Calluna vulgaris*: $W_m = 5.27$; *Juniperus communis*: $W_m = 4.24$; *Loiseleuria procumbens*: $W_m = 4.82$) were selected above their availability, perhaps as a consequence of the higher spatial overlap on this side between chamois and red deer, which make similar use of vegetal resources. Although competition among species is unlikely, due to the low population densities, over-exploitation of food resources and food niche overlap may be future limiting factors for local chamois population, and they should be taken into account for the proper management and control of wild and domestic ruminants.

As a result of a number of events of local extinction, natural dispersion and reintroductions, the Alpine subspecies of *Rupicapra rupicapra* (*R. r. rupicapra*) is now present throughout the European Alps, and locally in Slovenia and northwestern Croatia, Slovakia, Czech Republic, Vosges and Chartreuse Massif (France), numerous regions of Germany and even in New Zealand, with different population densities (Carnevali et al. 2009). The species usually lives in mountain areas, but it can show a high level of adaptability to a wide range of environments, from typical alpine environment to low-altitude river gorges, and it can be found even at sea level in New Zealand (Yockney and Hickling 2000) and in the Trieste Karst in Italy (Carnevali et al. 2009). In the Italian Alps, a population number of about 137 000 individuals has

been estimated. This number has been increasing in recent years, thanks to the creation of parks and other protected areas, substantial and progressive improvement of hunting management and numerous reintroduction and restocking projects. However, significant population declines have been observed in some Italian provinces, including Sondrio, where the present research has been carried out. The main reasons for local decline are the widespread human colonization of alpine territories, hunting pressure and competition from agriculture and livestock breeding (Carnevali et al. 2009). A reduction of niche breadth and a change of food habits of Alpine chamois have been observed in western Alps in response to the presence of sheep grazing in the same range (La Morgia and Bassano 2009), and livestock presence seems to induce the Pyrenean chamois *Rupicapra pyrenaica pyrenaica* to move to lower, forested areas (Herrero et al. 1996). Negative consequences on chamois populations can also be observed in response to the presence of sympatric wild herbivore species, which may induce chamois to use suboptimal feeding

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areas, as observed in central–eastern Alps in response to the presence of non-native mouflon *Ovis musimon* (Chirichella et al. 2013). The presence of interspecific competition was also observed by Lovari et al. (2014) between the Apennine chamois *R. p. ornata* and red deer *Cervus elaphus* in central Apennines (Italy), where a high degree of spatial and diet overlap between the two species was recorded. A high diet overlap between the Alpine chamois and red deer, both considered as intermediate feeders (Hofmann 1989), was also detected by Homolka and Heroldová (2001) in the Jeseníky Mountains (Czech Republic), by Bertolino et al. (2009) in the Italian western Alps and by Redjadj et al. (2014) in the French Alps, although in this case it did not lead to a competition phenomena.

Competition is not likely to occur between chamois and selective browser species, such as roe deer *Capreolus capreolus*, due to different feeding habits (Homolka 1996, Bertolino et al. 2009, Redjadj et al. 2014).

The onset of competition phenomena is dependent not only on diet similarity between herbivore species, but also on the availability of vegetal resources that can influence the choices made by the resident animal populations, in terms of food preferences, spatial behavior and habitat use and selection (Owen 1972). For example, researches carried out in the Swiss Alps suggest that competition may occur between Alpine chamois and ibex *Capra ibex* in winter, when resources are scarce, but not during other seasons, when vegetable biomass is abundant (Trutmann 2009).

The present research aims at describing the autumnal diet composition and food preferences of male and female Alpine chamois living in sympatry with red and roe deer in central Italian Alps by analysis of rumen contents available during the hunting season (September–November) and to confirm the following hypothesis: H1) as in autumn spatial segregation between genders is low, due to the approaching mating season, male and female diets are very similar in our samples; H2) chamois diet is more similar to red deer than to roe deer diet, due to the different feeding habits and habitat use of these species; H3) as a consequence of H2, palatable plant species are more positively selected by chamois in areas where spatial overlap with red deer is higher.

To test these hypotheses, the results of chamois rumen content analysis were integrated by data available from previous research on rumen content of red deer (Carabelli 2008) and roe deer (Del Vecchio 2012) and on space use of the three herbivore species (Canzi 2005) in the same study area.

Material and methods

Study area

Our data were collected in Val Fontana (surface area 7337 km², 9°59′ – 10°03′E; 46°12′ – 46°14′N), in the Province of Sondrio in the central Italian Alps. The Val Fontana extends from 500 m to approximately 3300 m a.s.l. This ample range of elevation determines the settlement and persistence of various vegetation climaxes, ranging from sub-mountain level to snow level (Credaro and Pirola 1975). The valley stretches from north to south, and therefore one

side is facing to the east (east side) and the other to the west (west side).

In addition to chamois, two other wild ungulate species are present in Val Fontana: red deer and roe deer. At the time of our study, the estimated pre-reproductive densities of chamois, red deer and roe deer in the study area were respectively 5.25 individuals/100 hectares, 2.99 individuals/100 hectares and 1.74 individuals/100 hectares of suitable surface area (Ferloni 2007). The recent trend of the populations of ungulates in Val Fontana is shown in Fig. 1.

The many pasture areas are shared by wild and domestic animals during summer, usually from June to September. Domestic animals include cattle, sheep and goats, horses and donkeys, and stocking rates vary over the years (Mattiello et al. 2003).

Rumen sampling and laboratory analysis

Thirty-five rumen samples were collected from culled chamois during the 2007 hunting season (4 September – 4 November). Table 1 lists details of the age classes and genders of these animals. Sample size corresponds to about 15% of the chamois estimated by direct count in the summer 2007 (230 chamois ≥ 1 year old).

In order to evaluate feeding overlap between chamois and other wild ungulate species, we used data from rumen samples of red deer (Carabelli 2008) and roe deer (Del Vecchio 2012) collected in the same area (Val Fontana) during a three-year project (hunting seasons 2005–2007). These data consisted of 82 rumen samples from red deer and 14 rumen samples from roe deer (see Table 1 for details on gender and age classes).

For the analysis of diet composition of chamois, red deer and roe deer, we used the same procedures, described below.

Rumen contents were mixed and at least 500 ml were collected by the hunters immediately after culling and stored at –20°C until analysis. The botanical composition of the diet was determined by the method of Homolka and Heroldová (1992): 25 ml of rumen contents were collected randomly from the initial sample; for each sample, all items were identified by stereomicroscopic examination, and the total volume of each component was determined by calibration. The

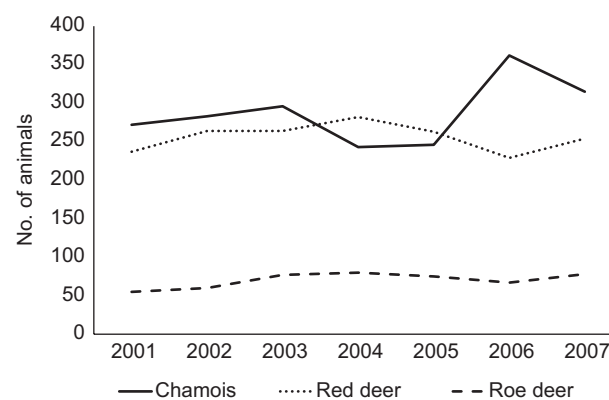


Figure 1. Trend of the populations of ungulates in the study area from 2001 to 2007 (data obtained from annual summer counts).

Table 1. Details of age classes and gender of culled chamois, red deer and roe deer whose rumen samples were analysed.

Age class	Chamois			Red deer			Roe deer		
	M	F	Tot.	M	F	Tot.	M	F	Tot.
Adults	9	10	19	4	27	31	5	2	7
Subadults	3	1	4	9	–	9	4	2	6
Yearlings	8	4	12	15	9	24	–	–	0
Calves/fawns	–	–	–	10	8	18	0	1	1
Tot.	20	15	35	38	44	82	9	5	14

percentage volume (%v) of each item over the total volume of the sample was calculated.

Plant parts were identified by comparison with photographs and drawings from existing literature sources (Della Beffa 1998, Fenaroli 1998, Pessot and Cusini 2007a, b) and with previously collected and classified photographs and slides of the flora from the study area. The work of Pignatti (1982) was followed for nomenclature.

Since the samples were already partially digested, we could seldom identify botanical species correctly, and sometimes only the genus or family of the vegetal items. We grouped monocotyledon species into 'Graminaceae, Juncaceae and Cyperaceae', fern species into 'Pteridophytes', and moss and lichens into 'Bryophytes'.

Resource availability

To collect data on vegetal resource availability in the areas used by chamois, we mapped the cull location of all sampled animals. The cullings were clearly separated into five groups (average distance between individuals in a group: 308.40 ± 108.92 m; average distance between group centroids: 6047.78 ± 2409.58 m). We then identified five areas around these groups and called them 'Areas of intensive study' (AIS), defined according to the minimum convex polygon method (MCP), i.e. by completely enclosing all culling locations, connecting the outer locations in such a way as to create a convex polygon (Mohr 1947). These AISs were: 'San Bernardo' (number and gender of culled chamois: two males, three females; 25.79 ha), 'Dalico' (six males, two females; 15.78 ha), 'Forame' (four males, six females; 25.75 ha), 'Laghi' (five males, one female; 14.58 ha) and 'Sareggio' (three males, three females; 14.64 ha). All the AISs were located between 1860 and 2500 m a.s.l. San Bernardo and Forame lie on the east side of the valley, and Dalico, Laghi and Sareggio on the west one.

To assess vegetal resource availability, we carried out a survey in summer 2011. Although rumen samples had been collected in autumn (i.e. during the hunting season), we decided to carry out the vegetation sampling in summer, i.e. during the period of peak production of the plants, in order to facilitate proper identification of species. Using ArcView 3.1, we generated a number of random points in order to have at least 0.4 points ha^{-1} for each AIS surface. Following Danova (2010), a trained observer estimated by eye plant species abundance as cover percentage of a circular plot (diameter 1 m) and stopped sampling when the increment curve built by adding the number of new species discovered at each survey was saturated (Pirola 1970). This procedure lead to a total of 209 surveys, distributed as follows: 54 in

San Bernardo, 38 in Dalico, 55 in Forame, 31 in Laghi and 31 in Sareggio.

We used several literature sources to identify plant species (Della Beffa 1998, Fenaroli 1998, Fanelli 2005, Ferranti 2005, Pessot and Cusini 2007a, b), and followed the work of Pignatti (1982) for nomenclature.

Statistical analysis

Prior to statistical analysis, bootstrap (i.e. resampling with replacement; $n = 1000$) was carried out on vegetable resource availability and diet compositions. This procedure is useful when sample size is small, as in our case, because it allows to calculate the real data distribution, without necessarily assuming that it follows a normal or Gauss distribution (Efron and Tibshirami 1993), and has already been successfully used in previous research on diet analysis (Macho and Lee-Thorp 2014).

New datasets generated by bootstrap resampling were used to calculate: 1) the average percentage coverage and 95% confidence intervals for each plant species in the AISs; 2) the average percentage volume and 95% confidence intervals for each identified vegetal food item in the rumen samples.

MANOVA tests were used to investigate the effects of AIS and valley side on vegetation availability, and the effects of gender (males versus females) and valley side on chamois diet composition.

The non-homogeneous distribution of samples among age classes did not allow reliable analysis of the age effect.

The niche breadth of chamois was calculated by the index of proportional similarity (PS; Feinsinger et al. 1981). This index takes into account the availability of resources and allows calculation of the degree of similarity between the frequency distribution of the resources used by chamois and that of available resources. The PS index is calculated as follows: $PS = 1 - 0.5 \sum |p_i - q_i|$, where: p_i is the proportion of resources used by the species; q_i is the proportion of resources available for that species. The index varies between 1, when the diet is as large as possible, meaning that the population exploits all available resources, and $|\min(q_i)|$, when the diet is the narrowest, meaning that the population focuses exclusively on rare resources, ignoring others.

To determine whether chamois showed a preference for a given plant species available in the study area, the diet selection index (W ; Manly et al. 1993) was calculated as follows: $W_i = o_i / p_i$, where: W_i is an indication of selection for the i th plant species, o_i is the proportion of use of that species, and p_i is the proportion of availability of the species. The reference value $W = 1$ indicates that the use of a plant species equals its availability. The average value of W (W_m) was calculated and associated with its 95% confidence intervals ($W_{inf} = W$ inferior; $W_{sup} = W$ superior) for each plant species. If the reference value falls outside the confidence interval of W_m , then the plant species is significantly over-used or under-used ($p < 0.05$); if the reference value falls within the confidence interval, then the use of the i th plant species equals its availability. We also calculated the diet selection indexes of chamois culled on the two valley sides, to study diet selection in relation to the different degree of spatial overlap with red deer.

To determine the diet overlap between chamois and red deer and between chamois and roe deer, Schoener's index (O) was used (Renkonen 1938, Schoener 1968). This is calculated as follows: $O_{jk} = 1 - 1/2 \sum |p_{ij} - p_{ik}|$, where: O_{jk} is the overlap between ungulate species j and k; p_{ij} is the proportion of use of the ith resource by the jth and kth species. Diet overlap between species j and k is complete when $O_{jk} = 1$ and absent when $O_{jk} = 0$ (Gordon and Illius 1989). To calculate these indexes, we used data on diet composition of red deer and roe deer already assessed in other studies in the same area with the same analytical approach (Carabelli 2008, Del Vecchio 2012).

Spatial overlap among chamois, red deer and roe deer in Val Fontana was studied by Canzi (2005) by means of direct observations at monthly intervals for a period of two years, at dawn and dusk, from four fixed observation points, two on each side of the valley and directed toward the opposite side. Canzi (2005) carried out a total of 96 observation sessions, each lasting 1 h 30 min (total observation time = 144 h), and recorded all sightings of red deer and other ungulate species on an IGM (Italian Military Geographic Institute) map (1:10 000) divided into grid units (GU = 500 × 500 m). Owing to the low roe deer density in the study area, only very few sightings of this species could be recorded. We therefore focused on red deer and chamois, and calculated the coefficient of spatial overlap (CSO; Berducou and Bousses 1985, modified by Bassano 1994) between these species as follows:

$CSO = \text{no. of grid units in common between red deer and chamois} / \text{no. of GU used by chamois (the species with the more limited spatial distribution)}$.

The CSO was calculated for each season and for each side of the valley.

Statistical analysis was carried out with Excel 2010 and SPSS 19.0.

Results

Resource availability

We found a total of 208 plant species belonging to 51 families in the AISs. In general, the AISs were characterized by extensive meadows and pastures (77.47% mean of coverage) alternating with shrubs (15.96%); trees (6.57%) on the lower borders of the AISs.

Graminaceae was the most representative family of the herbaceous layer (32.65%), followed by Compositae (8.47%), Rosaceae (5.22%), Cyperaceae (4.91%), Leguminosae (4.18%), Umbrelliferae (3.69%) and Juncaceae (2.69%). All other families were present with less than 2% of coverage. Shrubs were mainly represented by the Ericaceae family (12.67%). Among tree species, *Picea abies*, *Larix decidua* and *Alnus viridis* were the most abundant (2.63%, 1.98% and 0.92%, respectively).

We did not find any significant differences in the availability of vegetation among the AISs (Wilks' lambda = 0.006; F = 1.782; p = 0.08), but we did find them in the availability of vegetation according to valley side (Wilks' lambda = 0.025; F = 5.874; p = 0.032).

The plant species showing a significantly different coverage percentage on the two valley sides are listed in Table 2.

Diet composition, niche breadth and diet selection

Analysis of rumen contents revealed 26 species and 15 genera belonging to 21 plant families of the 51 available (41.18%) in the AISs.

Alpine chamois diet during autumn in the central Italian Alps is mainly based on the monocotyledon families (Graminaceae, Juncaceae and Cyperaceae group; 78.1% of diet volume). Other substantial families are Ericaceae (5.2%), Betulaceae (4.3%) and Cupressaceae (3.3%). Table 3 lists details of diet composition.

We did not find any significant differences in diet composition, either between valley sides (Wilks' lambda = 0.005; F = 6.047; p = 0.313) or between males and females (Wilks' lambda = 0.000; F = 124.223; p = 0.849).

The niche breadth index was PS = 0.61.

We found positive selections for Graminaceae, Juncaceae and Cyperaceae ($W_m = 2.10$; $W_{inf} = 1.96$; $W_{sup} = 2.24$), *Alnus viridis* ($W_m = 4.72$; $W_{inf} = 1.54$; $W_{sup} = 9.08$) and *Loiseleuria procumbens* ($W_m = 4.66$; $W_{inf} = 1.87$; $W_{sup} = 10.26$). Several species had negative selections (Table 4). The consumption of all other species was proportional to their availability (Table 5).

Some species (*Juniperus communis*, *Calluna vulgaris* and *Loiseleuria procumbens*) were positively selected only on the EAST side (Table 6).

Monocotyledons were positively selected on both sides (east: $W_m = 1.88$, $W_{inf} = 1.82$, $W_{sup} = 2.19$; west: $W_m = 2.02$, $W_{inf} = 1.78$, $W_{sup} = 2.13$).

Table 2. Coverage percentage of plant species on both sides of valley (only for species for which significant differences between sides were recorded).

Species	Coverage %		p
	East	West	
<i>Achillea millefolium</i>	1.73	1.17	0.000
<i>Alchemilla vulgaris</i>	1.33	0.02	0.061
<i>Anthoxanthum odoratum</i>	0.27	0.00	0.008
<i>Arnica montana</i>	0.07	0.39	0.024
<i>Avenella flexuosa</i>	0.57	0.00	0.021
<i>Briza media</i>	2.06	0.08	0.002
<i>Buplerum stellatum</i>	0.00	0.13	0.016
<i>Campanula barbata</i>	0.72	0.19	0.047
<i>Campanula scheuchzeri</i>	0.24	0.30	0.010
<i>Cerastium holosteoides</i>	0.13	0.00	0.071
<i>Festuca rubra</i>	5.91	2.34	0.000
<i>Festuca varia</i>	2.07	0.00	0.003
<i>Fragaria vesca</i>	0.75	0.06	0.025
<i>Galium aparine</i>	0.00	0.12	0.009
<i>Galium rubrum</i>	0.17	0.00	0.003
<i>Hieracium pilosella</i>	0.45	0.33	0.016
<i>Juniperus montana</i>	0.37	0.00	0.034
<i>Loiseleuria procumbens</i>	0.25	0.50	0.005
<i>Luzula campestris</i>	0.12	0.00	0.026
<i>Myosotis alpestris</i>	0.55	1.36	0.031
<i>Polygala alpina</i>	0.04	0.00	0.004
<i>Salix caprea</i>	0.18	0.44	0.030
<i>Trifolium alpinum</i>	0.68	1.60	0.000
<i>Veronica officinalis</i>	0.18	0.00	0.004

Table 3. Families, genera and species in autumn diet composition of Alpine chamois in central Italian Alps (% of volume diet \pm SE).

Family	% \pm SE	Genus/species	% \pm SE
Betulaceae	4.32 \pm 1.60	<i>Alnus viridis</i>	4.32 \pm 1.60
Bryophytes	1.79 \pm 0.55	moss and lichens	1.79 \pm 0.55
Caryophyllaceae	0.03 \pm 0.03	<i>Silene</i> sp.	0.03 \pm 0.03
Compositae	0.39 \pm 0.13	<i>Arnica montana</i>	0.05 \pm 0.05
		<i>Artemisia</i> sp.	0.04 \pm 0.03
		<i>Cirsium</i> sp.	0.09 \pm 0.05
		<i>Hieracium</i> sp.	0.01 \pm 0.01
		<i>Homogyne alpina</i>	0.11 \pm 0.09
Crassulaceae	0.14 \pm 0.06	<i>Sedum rizoides</i>	0.11 \pm 0.06
		<i>Sempervivum montanum</i>	0.03 \pm 0.02
Cupressaceae	3.37 \pm 1.25	<i>Juniperus communis</i>	3.37 \pm 1.25
Ericaceae	5.30 \pm 1.03	<i>Arcostaphylos uva-ursi</i>	0.16 \pm 0.11
		<i>Calluna vulgaris</i>	0.36 \pm 0.12
		<i>Loiseleuria procumbens</i>	1.95 \pm 0.97
		<i>Rhododendron ferrugineum</i>	0.23 \pm 0.14
		<i>Vaccinium myrtillus</i>	0.71 \pm 0.27
		<i>Vaccinium uliginosum</i>	0.05 \pm 0.03
		<i>Vaccinium vitis-idaea</i>	1.28 \pm 0.34
		<i>Vaccinium</i> sp.	0.67 \pm 0.42
Leguminosae	0.14 \pm 0.12	<i>Lotus alpinus</i>	0.01 \pm 0.01
		<i>Trifolium</i> sp.	0.12 \pm 0.11
		<i>Vicia</i> sp.	0.01 \pm 0.01
Geraniaceae	0.01 \pm 0.01	<i>Geranium sylvaticum</i>	0.01 \pm 0.01
Graminaceae, Juncaceae, Cyperaceae	78.11 \pm 2.35	Graminaceae, Juncaceae, Cyperaceae	78.11 \pm 2.35
Lamiaceae	0.20 \pm 0.11	<i>Thymus serpyllum</i>	0.20 \pm 0.11
Pinaceae	0.64 \pm 0.21	<i>Larix decidua</i>	0.18 \pm 0.05
		<i>Picea abies</i>	0.46 \pm 0.22
Plantaginaceae	0.08 \pm 0.07	<i>Plantago media</i>	0.08 \pm 0.07
Polygonaceae	0.02 \pm 0.01	<i>Rumex</i> sp.	0.02 \pm 0.01
Primulaceae	0.11 \pm 0.09	<i>Primula</i> sp.	0.02 \pm 0.01
		<i>Soldanella alpina</i>	0.09 \pm 0.08
Pteridophytes	1.36 \pm 0.68	Pteridophyte	1.36 \pm 0.68
Ranunculaceae	0.02 \pm 0.01	<i>Clematis alpina</i>	0.01 \pm 0.01
		<i>Ranunculus</i> sp.	0.01 \pm 0.01
Rosaceae	0.96 \pm 0.37	<i>Alchemilla vulgaris</i>	0.01 \pm 0.01
		<i>Cotoneaster nebrodensis</i>	0.06 \pm 0.05
		<i>Geum montanum</i>	0.01 \pm 0.01
		<i>Potentilla</i> sp.	0.10 \pm 0.05
		<i>Rubus idaeus</i>	0.78 \pm 0.37
Rubiaceae	0.02 \pm 0.02	<i>Galium</i> sp.	0.02 \pm 0.01
Salicaceae	0.29 \pm 0.12	<i>Salix</i> sp.	0.29 \pm 0.12
Saxifragaceae	0.33 \pm 0.17	<i>Saxifraga</i> sp.	0.33 \pm 0.17
Umbrelliferae	0.09 \pm 0.06	<i>Meum</i> sp.	0.09 \pm 0.06
Urticaceae	0.04 \pm 0.04	<i>Urtica dioica</i>	0.04 \pm 0.04
Violaceae	0.01 \pm 0.01	<i>Viola</i> sp.	0.01 \pm 0.01

Diet and spatial overlap with other species

The O index was 0.233 for chamois versus roe deer and 0.603 for chamois versus red deer.

Figure 2 shows the CSO between chamois and red deer for each valley side according to season. The overlap was always found to be higher on the east side, where all the grid units used by red deer were used also by chamois in summer and in autumn.

Discussion and conclusions

Our results confirm that the autumn diet of chamois is based mainly on monocotyledon species, in agreement with the

results of many other studies (Schröder 1977, Perle and Hamr 1985, García-González and Cuartas 1996, Homolka and Heroldová 2001, Bertolino et al. 2009, Trutmann 2009). The high percentage of consumption of monocotyledons in our samples (78.11% of total diet volume) may be related to their availability in the environment used by chamois during the hunting season in the study area (e.g. high open pasture rich in species belonging to the Graminaceae and Cyperaceae families). In these areas, monocotyledon species are more palatable, when compared with lower altitudes, due to the phenological shift as late snow melts (Cornelius et al. 2013). These species were over-used compared to their availability (as indicated by the W index), possibly because part of these resources was extensively used by grazing flocks of sheep from neighboring Switzerland. The spatial overlap of these

Table 4. Genera and species negatively selected according to W index; W_m = mean; W_{inf} = inferior; W_{sup} = superior.

Genera/species	W_m	W_{inf}	W_{sup}
<i>Alchemilla vulgaris</i>	0.01	0.00	0.01
<i>Arcostaphylos uva-ursi</i>	0.11	0.00	0.28
<i>Arnica montana</i>	0.23	0.00	0.69
<i>Artemisia</i> sp.	0.21	0.00	0.53
<i>Cirsium</i> sp.	0.18	0.00	0.42
<i>Clematis alpina</i>	0.01	0.00	0.04
<i>Galium</i> sp.	0.02	0.00	0.05
<i>Geranium sylvaticum</i>	0.02	0.00	0.06
<i>Geum montanum</i>	0.02	0.00	0.05
<i>Hieracium</i> sp.	0.01	0.00	0.02
<i>Homogyne alpina</i>	0.20	0.00	0.54
<i>Larix decidua</i>	0.09	0.04	0.14
<i>Lotus alpinus</i>	0.01	0.00	0.02
<i>Picea abies</i>	0.18	0.04	0.34
<i>Potentilla</i> sp.	0.03	0.01	0.06
<i>Primula</i> sp.	0.05	0.00	0.14
<i>Ranunculus</i> sp.	0.01	0.00	0.01
<i>Rhododendron ferrugineum</i>	0.05	0.00	0.12
<i>Rumex</i> sp.	0.02	0.00	0.05
<i>Sedum</i> sp.	0.30	0.06	0.67
<i>Sempervivum montanum</i>	0.13	0.00	0.31
<i>Silene</i> sp.	0.14	0.00	0.41
<i>Thymus serpyllum</i>	0.27	0.04	0.65
<i>Trifolium</i> sp.	0.05	0.00	0.16
<i>Urtica dioica</i>	0.06	0.00	0.19
<i>Vaccinium myrtillus</i>	0.33	0.08	0.66
<i>Vaccinium uliginosum</i>	0.02	0.00	0.04
<i>Vicia</i> sp.	0.05	0.00	0.16
<i>Viola</i> sp.	0.01	0.00	0.01

flocks with the chamois in our study area was observed during the annual population count. This overlap was apparent also by analysis of the health status of chamois in Val Fontana, which revealed the presence of parasites typical of sheep in chamois (Andreoli 2008); some of the analyzed chamois were the same as those used for this study on diet. Although the hypothesis of feeding interactions between chamois and sheep cannot be confirmed by our data (because we did not analyze sheep diet), it is supported by the work by Herrero et al. (1996) and La Morgia and Bassano (2009). These last authors suggest that the presence of sheep may lead to an increase of the percentage of monocotyledons in the diet of chamois, as a response to the reduced availability of highly digestible forbs.

Table 5. Families, groups, genera and species used in proportion to availability according to W index; W_m = mean; W_{inf} = inferior; W_{sup} = superior.

Families/groups/genera/species	W_m	W_{inf}	W_{sup}
Bryophytes	0.85	0.29	1.42
<i>Calluna vulgaris</i>	0.91	0.25	1.89
<i>Cotoneaster</i> sp.	0.50	0.01	1.34
<i>Meum</i> sp.	0.56	0.00	1.48
<i>Plantago media</i>	0.38	0.00	1.12
Pteridophytes	1.14	0.20	2.63
<i>Rubus idaeus</i>	1.46	0.22	2.90
<i>Salix</i> sp.	0.56	0.14	1.05
<i>Saxifraga</i> sp.	1.32	0.30	2.77
<i>Soldanella alpina</i>	0.27	0.00	0.81
<i>Vaccinium vitis-idaea</i>	1.35	0.71	2.06

Table 6. Species differently selected according to W index on both sides of valley; W_m = mean; W_{inf} = inferior; W_{sup} = superior.

Species	East			West		
	W_m	W_{inf}	W_{sup}	W_m	W_{inf}	W_{sup}
<i>Juniperus communis</i>	4.24	1.16	6.08	0.62	0.22	1.17
<i>Calluna vulgaris</i>	5.27	1.04	9.12	0.18	0.11	1.31
<i>Loiseleuria procumbens</i>	4.82	1.02	7.97	0.82	0.51	3.92

Shrub and tree families (Ericaceae, Betulaceae, Cupressaceae, Salicaceae, Pinaceae) are also present in the chamois diet, but play a modest role in autumn, as reported by Mustoni et al. (2002), although in winter they may become more substantial (García-González and Cuartas 1996, Mustoni et al. 2002, Trutmann 2009). In our study, Ericaceae was the most frequently represented shrub family in chamois diet. Within this family, Alpine azalea *Loiseleuria procumbens* was particularly appreciated (1.95% of total diet volume), although its consumption has never been reported in previous studies on chamois diet. The W_m index for this species was high (4.66), indicating that chamois have a true preference for this plant. *Alnus viridis* was positively selected (4.32% of total diet volume; W index = 4.72), but this may be due to the scarcity of this tree within the AISs, since it is typical of lower altitudes. However, its presence in diet composition indicates that it is quite palatable for chamois, as they have to search for it. Pinaceae (*Picea abies* and *Larix decidua*) were also found, but were negatively selected and less frequently consumed than reported in other studies in the Pyrenees on *R. p. pyrenaica* (García-González and Cuartas 1996). This may be due to a relation between increased consumption of conifers in the diet and snowfalls, which are abundant in the Pyrenees but not in our study area during the autumn hunting season. We recorded a relatively low consumption of herbaceous plants (other than Gramineae, Cyperaceae and Juncaceae), such as Ranunculaceae, Primulaceae, Umbrelliferae, Leguminosae and Compositae (Table 3), perhaps due to the low palatability of these species during the study period.

The value of the niche breadth index again confirms that chamois do not use all available resources and, in some cases, even exploit selected species above their availability.

In agreement with our first hypothesis (H1), we found no differences in diet composition between genders. This

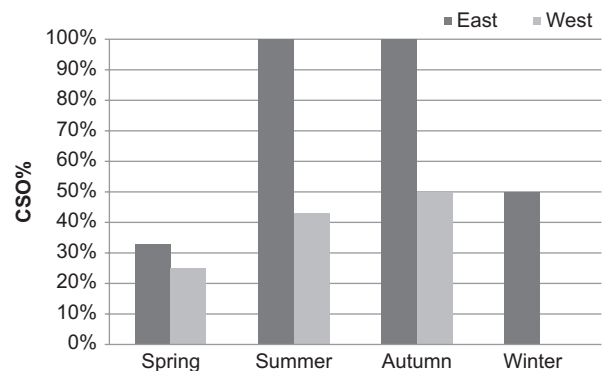


Figure 2. Coefficient of spatial overlap between chamois and red deer for each valley side according to season.

could be expected, because the approach of the mating season moved males and females to use the same areas and share the same food resources. In fact, both males and females were culled in each AIS. This is in agreement also with the behavioral observations reported by Ferretti et al. (2014), who assessed a similar use of vegetation types (mainly palatable graminoids) by both genders in autumn. However, our sample size was small, therefore we cannot exclude that the absence of differences could be due also to the limited number of samples.

Our results on diet overlap between chamois and other ungulate species met our prediction (H2): the diet of chamois was more similar to that of red deer than to that of roe deer. This is in agreement with the results of other studies on inter-specific trophic interactions (Homolka and Heroldová 2001, Bertolino et al. 2009, Redjadj et al. 2014). Both red deer and chamois are intermediate feeders and, in our study area, they fed mainly on monocotyledons during our study period. However, monocotyledons represented only half the volume percentage of rumen contents in red deer, and broad-leaved and shrub species were frequently found in their diet (24.88% and 17.29% of total diet volume, respectively; Carabelli 2008). This is probably due to the fact that in Val Fontana red deer show a wider altitude range and also use woodland areas in autumn (Mattiello et al. 1997), and has therefore access to food resources that are less available for chamois. This may explain why diet overlap is relatively high, but some differences are still present between the two species. As expected, diet overlap with roe deer was low. This is most likely due to the different habitats frequented by the two ungulate species in our study area. In fact, roe deer usually lives at lower altitudes, in habitats below the tree line, very different from those frequented by chamois. As a result, the composition of roe deer diet mainly included seeds, fruits, leaves and sprouts of broad-leaved species (47.11% of total diet volume) and shrubs (23.29% of total diet volume), whereas monocotyledons represented only 12.96% of total diet volume (Del Vecchio 2012). Although based only on few rumen samples, our results seem to be perfectly aligned with the results reported by other authors (Homolka 1996, Bertolino et al. 2009), who found a limited overlap of the roe deer food niche with other species such as red deer, chamois and mouflon.

As H2 was verified, we tried to confirm our third prediction (H3). We observed a higher spatial overlap between chamois and red deer on the east side, which was extremely high in summer and in autumn, when our rumen samples were collected. This was probably due to the fact that, in alpine environment, chamois frequently use high-altitude bands on both sides, whereas red deer make a more frequent use of high-altitude bands on east than on west (Canzi 2005). On west, red deer more frequently use low-altitude bands, so spatial overlap with chamois is less common on this side. Therefore, according to our prediction, we expected to observe a more pronounced positive selection for some palatable species on east. This was true for three species that were present in the diet of both chamois and red deer (Carabelli 2008): *Juniperus communis*, *Calluna vulgaris* and *Loiseleuria procumbens*. These species were positively selected on the east valley side, whereas the same plants were selected according to availability on the west side.

Based on our results, we suggest that there may be a potential for competition between chamois and red deer, in particular for monocotyledons, which are positively selected by chamois and palatable for both species, and for some palatable species which are not common in the study area. This potential seems to be higher on the East side of the valley, where we observed a higher degree of spatial overlap between the two herbivore species. However, we acknowledge that our data are unfortunately based on a limited number of rumen samples (due to difficulties in field data collection), and on observations at dawn and dusk, which possibly lead to missing information on space use during nocturnal activity of the animals, and therefore space overlap may have been underestimated. Furthermore, the population trend of the three ungulate species in Val Fontana (Fig. 1) is regular, with small oscillations from year to year, and no sudden drop is observed in any species in relation to the increase of other species. Under these conditions, it is unlikely that competition between species is occurring. Studies on resource sharing between chamois and red deer in Val Fontana certainly need to be further promoted, as inter-specific competition has already been verified between red deer and the Apennine chamois in central Italian Apennines, where both spatial and diet overlap were recorded (Lovari et al. 2014).

The populations of Alpine chamois are currently not at risk of extinction, but population declines have been observed in some areas. Exploitation of food resources and food niche overlap may be limiting factors for local populations of chamois and should be considered in the management and control of the wild and domestic ruminants in our study area.

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