

Diet composition of alpine chamois (*Rupicapra rupicapra* L.): Is there evidence for forage competition to the alpine ibex (*Capra ibex* L.)?

Master Thesis in Ecology at University of Zurich by
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Abstract

Competition between animal species (interspecific competition) occurs when two or more species inhabit the same habitat and use a common and limited resource the same way. Competition primarily affects the individuals by reducing fecundity, growth and survival rates, but depending on the strength, also the population dynamics of the competing species are influenced. In some parts of the valleys of Trupchun and Müschauns in the Swiss National Park (SNP) chamois and ibex are living in the same constraint area without obvious separation of their habitats. Since a survey on the forage composition of ibex was conducted, the interest on the dietary composition of chamois arose to investigate if forage competition between this two species occurs. Therefore I conducted micro-histological faecal analysis for chamois forage and compared the results with the data obtained from the ibex. The samples were collected in February, May, August and November 2008 to investigate the diet in all four seasons. Chamois fed most frequently on graminoids regardless of the season, whereas the amount of herbs significantly increased from winter to summer. *Ericaceae* species were present in the chamois diet during the whole year, but were most frequently consumed in autumn. The conifer consumption was the highest in winter and decreased to almost negligible amounts in summer and autumn. There was a significant difference between chamois and ibex forage in winter, but not in spring, summer and autumn. These findings indicate that chamois and ibex feed on the same forage in seasons when plenty biomass is available but separate to different forages in winter when resources are scarce and competition seem to occur.

Zusammenfassung

Konkurrenz zwischen Tierarten (interspezifische Konkurrenz) entsteht, wenn sie ein gleiches Habitat bewohnen und eine limitierte Ressource auf die gleiche Art und Weise nützen. In erster Linie verursacht Konkurrenz eine Reduktion von Wachstum, Fruchtbarkeit und Überlebenswahrscheinlichkeit der Individuen einer Tierart, aber je nach Stärke der Konkurrenz ist auch die Populationsdynamik betroffen. Im Val Trupchun und Val Müschauns im Schweizerischen Nationalpark (SNP) leben Gämse und Steinböcke in grosser Zahl, ohne dass eine eindeutige Separation ihrer Habitate ersichtlich ist. Weil kürzlich eine Studie zur Nahrungszusammensetzung des Alpensteinbockes durchgeführt wurde, ist das Interesse aufgetaucht, auch die Nahrungszusammensetzung der Gämse zu ermitteln um eine mögliche Nahrungskonkurrenz zwischen diesen zwei Arten zu erforschen. Aus diesem Grund habe ich eine mikrohistologische Kotanalyse der Gämse durchgeführt und die Ergebnisse mit der Nahrungszusammensetzung des Steinbockes verglichen. Die Proben wurden im Februar, Mai, August und November 2008 gesammelt um einen Überblick über das ganze Jahr zu erhalten. Die Gämse haben das ganze Jahr über am häufigsten Graminoiden gefressen, während der Anteil der Kräuter vom Winter zum Sommer stark zugenommen hat. *Ericaceae* Arten wurden am häufigsten im Herbst gefressen, waren aber das ganze Jahr über in der Nahrung der Gämse zu finden. Der Anteil der Koniferen war im Winter am grössten und hat im Laufe des Jahres so stark abgenommen, dass im Sommer und Herbst nur noch vernachlässigbar kleine Anteile zu finden waren. Einen signifikanten Unterschied zwischen den Nahrungszusammensetzungen von Gämse und Steinbock konnte im Winter gefunden werden, aber nicht im Frühling, Sommer oder Herbst. Diese Ergebnisse deuten darauf hin, dass Gämse und Steinböcke in den Jahreszeiten, in denen genügend Nahrungsressourcen vorhanden sind, das gleiche Futter fressen, während die Nahrungsknappheit im Winter Konkurrenz verursacht und eine Ressourcenteilung bewirkt.

Introduction

One of the most essential activities of an animal is the consumption of forage (Gordon 2003). For an organism it is important to optimize forage intake and diet selection to meet the nutrient demands for survival, growth and reproduction (Gordon 2003). However, since terrestrial ecosystems are inhabited by a multitude of different vertebrate and invertebrate animal species, interactions when exploiting resources are unavoidable and negative interactions such as competition are very likely to occur (Connell 1980). Competition between species (interspecific competition) occurs when two or more species inhabit the same habitat and use a common and limited resource the same way (de Boer and Prins 1990). Primarily it affects the individuals by reducing fecundity, growth and survival rates, but consequently, depending on the strength, also the population dynamics of the competing species are influenced (Hardin 1960, Townsend et al. 2003). To avoid competition, animals need to occupy a unique ecological niche. Among competing animal species, this may happen by diverging in habitat choice (habitat shift) or by adaptations to exploit a particular forage resource (e.g., species specific beak properties for particular seed sizes in granivores; Connell 1980, Schoener 1982). However, as a consequence, competition has an impact on the evolution and distribution of animal species (Schoener 1982, Townsend et al. 2003).

Among animal species feeding on plant material, invertebrates as well as vertebrates are affected by competition for a common forage resource (Brown and Davidson 1977, Albrecht and Gotelli 2001). Yet, even if an overlap in diet and habitat use at a certain time of the season can be detected, it is important to investigate how this overlap varies over time, since plant growth and productivity are strongly influenced by variation of temperature and precipitation and therefore the biomass produced considerably varies over the course of the year and between years (Klein 1965, Briggs and Knapp 1995, Post and Stenseth 1999, Nippert et al. 2006). Thus, competition for forage might considerably differ between seasons of high forage quality and quantity and seasons of forage scarcity.

Many studies have been conducted on forage selection and dietary overlap of domestic and wild herbivores as well as combinations of both groups in various ecosystems (Prins and Fritz 2008; also see e.g., Sinclair 1985, Jenkins and Wright 1988, Heroldova 1996, Homolka 1996, Voeten and Prins 1999, Baldi et al. 2001, Mysterud 2000, Homolka and Heroldova 2001, Bagchi et al. 2004, Madhusudan 2004, Retzer 2007, Zhongqiu et al. 2008). Evidence for competition among wild native herbivores has been quite rarely identified, while studies investigating habitat and forage overlap between native herbivores and introduced ones, almost always found indication for competition between the species. For example, competition was recorded between chamois (*Rupicapra rupicapra* L.) and alpine ibex (*Capra ibex* L.) in the Hochlantsch Mountains (Schröder and Kofler 1984), when ibex were introduced in an area where previously only native chamois had lived. The authors found that after the introduction both species occupied the same habitats with regard to geographic features and had a rather high overlap in forage. As a consequence, the number of chamois decreased severely leading the authors to the conclusion that competition between these two species occurred.

In the Swiss National Park (SNP), founded in 1914, the alpine ibex became extinct in the 17th century. In 1920 a few individuals were re-introduced into this area and the population increased considerably (Buchli and Abderhalden 1998). Today chamois and ibex inhabit the SNP in high densities and without natural population control through predators. Long-term observations in the valleys of Trupchun and Müschauns have shown that chamois and ibex occupy the same habitat. Since a survey on the composition of ibex forage was conducted for wildlife conservation purposes, the interest arose to do the same with the chamois forage to investigate potential competitive interactions between these two species. Therefore, the aims of my study were to determine the composition of chamois forage and how it changes over the course of a year. Further, I compared the forage composition of chamois and ibex (ibex data provided by Zingg 2009) to assess whether there is evidence for competition.

Methods

Animal species under study

Both animals under study, chamois and ibex, belong to the family of the *Bovidae*. The recent bovids are defined as a consistent group, however, the classification and the number of species per genera is not very clear. Two genera contained within this family (*Capra* and *Rupicapra*) are known as mountainous animals in Europe. In the literature, some authors divide them into different subfamilies, others classify them into the same subfamily, but into different tribes: *Rupicaprinae* (*Rupicaprini*) with *Rupicapra* and *Caprinae* (*Caprini*) with *Capra* among others (Niethammer and Krapp 1986; Figure 1)

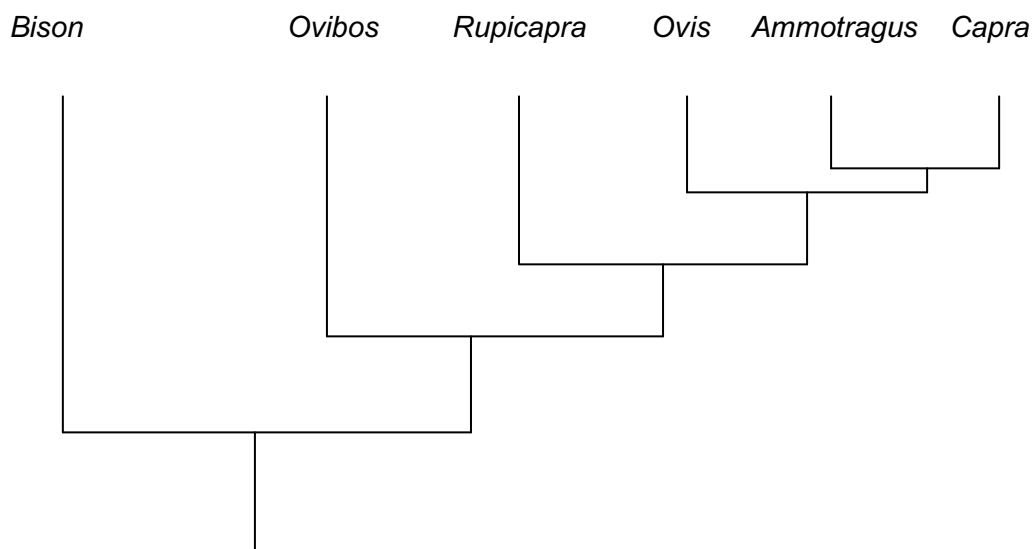


Figure 1: Cladogram of the European *Bovid* genera. The genus *Bison* forms a separate subfamily (*Bovinae*), the other five genera are either divided into three subfamilies or they are treated as one subfamily (*Caprinae*) with three distinct tribes: *Ovibovinae* (*Ovibovini*) with *Ovis*, *Rupicaprinae* (*Rupicaprini*) with *Rupicapra* and the *Caprinae* (*Caprini*) with *Ovis*, *Capra* and *Ammotragus* (Niethammer and Krapp, 1986).

Both chamois and ibex are distributed across Europe; however, they are restricted to mountainous areas and were influenced by extinction and resettlement processes throughout the last centuries. Among the European chamois, two species (*Rupicapra rupicapra* L. and

Rupicapra pyrenaica Bonaparte) and 10 subspecies are distinct (Shackleton et al. 1997), which all originated from isolation on separate mountain ranges (Bögel 2001). The alpine chamois (*Rupicapra rupicapra*) weights between 35 and 40 kg and has a shoulder height of 70 to 90 cm; there is no or just a small sexual dimorphism (somewhat bigger and heavier males compared to females; Sägesser and Krapp 1986). The alpine ibex (*Capra ibex* L.) in contrast, show a strong sexual dimorphism, which is characterized by differences of the horns, the chin-beard of the males, different body weights (males 70 – 120 kg, females 40 – 50 kg) and body lengths (head to trunk length of males roughly 140 cm, females roughly 115 cm; Nievergelt and Zingg 1986, Neuhaus and Ruckstuhl 2002, Abderhalden 2005)

Concerning habitat selection chamois are quite adaptable (Reimoser 2002). The summer habitat ranges from cliffy areas to high alpine plateaus, steep grass areas and subalpine mountain forests (Sägesser and Krapp 1986, Bögel 2001). However, the alpine plateaus seem to be the preferred areas (Sägesser and Krapp 1986). Because of the low slope, snow cover is high on these plateaus during winter, which forces the animals to migrate to lower elevations, where snow cover is lower. During winter they mostly stay in forested areas below the timberline, where they also find better protection against wind and cold (Sägesser and Krapp 1986, Bögel 2001). The summer habitat of the ibex is characterized by steep and rocky areas, yet, they are also observed in open and sunny subalpine forests interspersed with rocks. Steep and southerly exposed slopes with low snow cover generally serve as winter ranges (Nievergelt and Zingg 1986, Meile et al. 2003).

Study site

My study areas were the valleys of Müschauns and Trupchun that are part of the SNP. The SNP is located in the Engadine valley of the Central Alps. The park is a mountainous region ranging from 1400 to 3174 m above sea level (a.s.l.) in elevation and consisting of 50% scree and rocks, 21% alpine and subalpine grasslands and 29% coniferous forest on an area of 170 km² (Schütz et al. 2000). The tree line is at approximately

2200 m a.s.l. and the forest is dominated by *Pinus cembra* L. and *Larix decidua* Mill. (Saether et al. 2002). Measurements at the meteorological station Buffalora (1970 m a.s.l.) between 1959 and 2007 showed an annual mean temperature of 0.57 ± 0.59 °C (mean \pm std. dev.) and an average yearly precipitation of 868.8 ± 155.89 mm, with means of 46.52 ± 33.15 mm and 106.48 ± 35.42 mm in January and July, respectively. The chamois population inhabiting the valleys of Trupchun and Müschauns display a remarkable numeric constancy (from 1960 to 2008: 171.7 ± 36.5 individuals (mean \pm std. dev.), Figure 2; Boschi and Nievergelt 2003), whereas the ibex population is larger and fluctuates more (245.4 ± 82.0 individuals; Figure 2). These two species inhabit the valleys throughout the entire year (Figure 3 and 4), but migrate in altitude. The third ungulate species, red deer (*Cervus elaphus* L.) also occurs frequently in the study area during the summer (388.5 ± 117.9 individuals, Figure 2), but leaves the park at the beginning of winter (Suter et al. 2004).

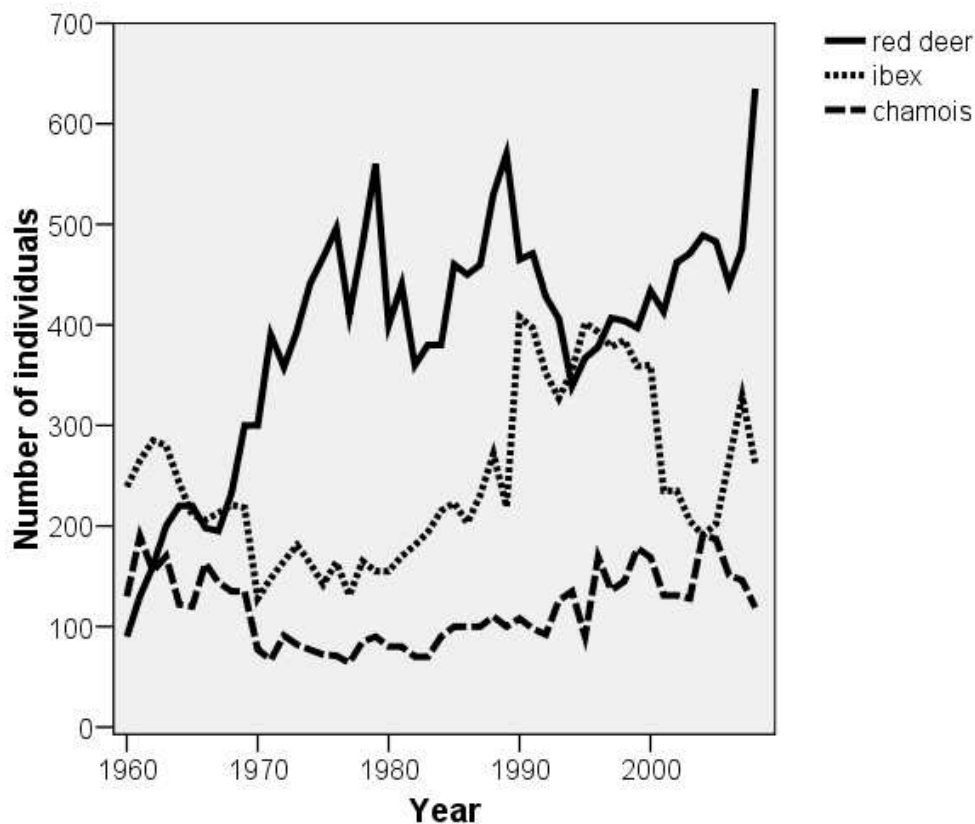


Figure 2: Population numbers of chamois, ibex and red deer in the valleys of Trupchun and Müschauns between 1960 and 2008 (SNP, unpublished data).

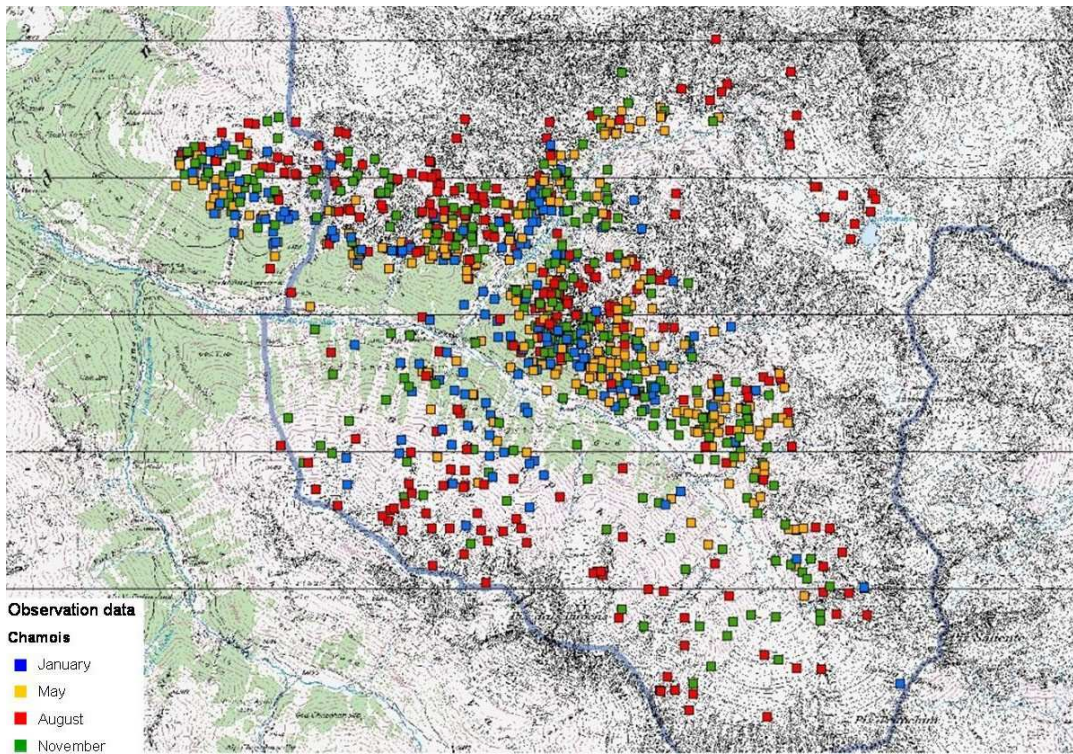


Figure 3: Chamois observations in the valleys of Trupchun and Müschauns from 1997 to 2005 (Haller 2006).

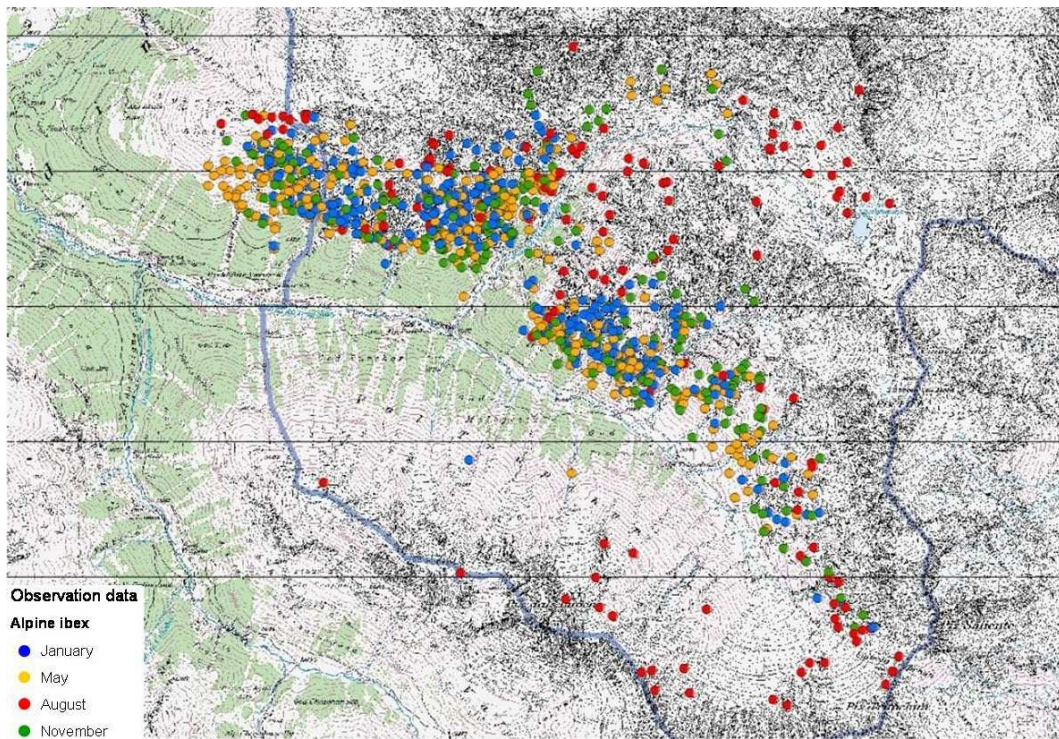


Figure 4: Ibex observations in the valleys of Trupchun and Müschauns from 1997 to 2005 (Haller 2006).

Field sampling

Twenty fresh dung samples of both chamois and ibex, respectively, were collected four times throughout the year: February 12th, May 22nd, August 20th and November 18th, 2008. The dung was sampled randomly by walking transects in areas where both animal species were previously observed. The transects started at the valley bottom and went straight up the mountain, with some compromises due to the accessibility of the terrain. The width of a transect was 10 m and I walked as many transects as necessary to obtain the 20 samples. Pellet groups found in this area were assigned either to chamois, ibex or other ungulates and one pellet group was defined as one sample. To be included into the collection the samples had to be separated by a minimum distance of 10 m.

Laboratory analysis of dung samples

To keep the samples from decomposing they were stored in a freezer at –20 °C until they were processed in an autoclave. After autoclaving, the pellets were crushed and ground in a mortar. From each grounded sample 2.5 g were taken, covered with distilled water, mixed in a lab blender and finally rinsed through a sieve with 0.1 mm mesh width. The residue was first washed with water and afterwards with 70% alcohol. Then it was transferred into alcohol (70%) in which the samples were stored.

To determine the epidermal fragments contained in the samples, the alcohol mixture was poured into a petri dish and allowed to settle for 15 min. I then took a random drop with a pipette and transferred it to a microscope slide. The drop was covered and viewed at a magnification of 200x (see also Suter et al. 2004). On each slide 10 epidermal fragments with a minimum area of 0.02 mm² were identified to the individual species, a genera or group of several species (see Table 1) along two transects starting at the left and the top of the slide respectively. This procedure was repeated 10 times for each sample. Thus, a total of 8000 fragments (i.e., 10 fragments per slide x 10 grab samples from 80 samples) were analysed for each animal species.

Over the last few decades, the preparation of material for micro-histological faecal analyses has varied considerably (Vavra and Holechek 1980). Some researchers boiled their samples or even added different reagents (color) to highlight some plant cell features (Zyznar and Urness 1969, Laitat 1983, Norbury 1988, Katona and Altbäcker 2002), whereas others emphasized the different digestibility among herbs, graminoids (Garcia-Gonzalez 1983), shrubs and conifers and proposed correction factors for compensation (Dearden et al. 1975, Putman 1984, Jordi et al. 1995). However, because a consensus about the treatments was not obvious, my samples remained untreated and I disclaimed operating with correction factors.

Table 1: Plant species, genera and species groups identified in faecal pellets of chamois and ibex. Names in parentheses indicate species or genera with similar epidermis characteristics that are difficult to identify.

Graminoids:	
<i>Cyperaceae</i>	<i>Carex</i> sp. <i>Elyna myosuroides</i> (Vill.) Fritsch unknown <i>Cyperaceae</i>
<i>Poaceae:</i>	<i>Festuca ovina</i> L. <i>Festuca rubra</i> L./ <i>F. violacea</i> Gaudin <i>Festuca</i> sp. <i>Nardus stricta</i> L. <i>Sesleria caerulea</i> (L.) Ard. <i>Agrostis capillaris</i> L./ <i>Anthoxanthum odoratum</i> L./ <i>Dactylis glomerata</i> L./ <i>Trisetum flavescens</i> (L.) P. Beauv., (<i>Briza media</i> L.) = group 1 <i>Deschampsia caespitosa</i> (L.) P. Beauv./ <i>D. flexuosa</i> (L.) Trin./ <i>Phleum alpinum</i> L., (<i>Helictotrichon pubescens</i> (Huds.) Pilg., <i>Briza media</i>) = group 2 <i>Poa pratensis</i> L., (<i>Helictotrichon pubescens</i>) = group 3 unknown <i>Poaceae</i>
<hr/>	
Dicots:	
	Herbs
<i>Ericaceae</i>	<i>Erica carnea</i> L. <i>Rhododendron</i> sp. <i>Vaccinium myrtillus</i> L. <i>Vaccinium vitis-idaea</i> L. unknown <i>Ericaceae</i> unknown dicots
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Conifers:	
<i>Cupressaceae</i>	<i>Juniperus communis</i> L.
<i>Pinaceae</i>	<i>Larix decidua</i> Mill. <i>Picea abies</i> (L.) H. Karst. <i>Pinus</i> sp. unknown conifers
<hr/>	
Others:	
	ferns mosses unknown fragments
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Reference slides for epidermal fragments of different plant species

For identifying the plant fragments I used references from a database (<http://wwwtest.wsl.ch/kotanalyse/kotanalyse/anmelden.html>) that provides slides for epidermal faecal analyses. I additionally collected leaf material of plants potentially consumed by chamois and ibex and not yet included in the database and prepared the reference slides as following: The leaves were cut into small pieces (0.5 cm²) and bleached in 2.5% sodium-hypochlorite (javel water) for several hours up to several days until the epidermis could be removed. The fragments were then placed on a microscope slide and preserved with a layer of glycerine. The cover slide was fixed with nail polish.

Statistical analyses

To assess in- and decreases of some of the plant groups consumed by chamois in dependence of the seasons, the total numbers of *Cyperaceae*, *Poaceae*, herbs, *Ericaceae*, unknown dicots, conifers and others (including ferns, mosses and unknown fragments) were log(x+1) transformed to fulfil the homogeneity and normality criteria and analysed in a one-way ANOVA with a Tukey Honestly Significant Difference (HSD) posthoc test for multiple analysis. The plant groups were the independent and the seasons the dependent variables.

To assess differences in forage composition and season simultaneously, the plant species or groups contributing to more than 5% to the chamois forage in either season were log(x+1) transformed to fulfil the homogeneity and normality criteria and analysed by a Detrended Correspondence Analysis (DCA; CANOCO 4.5; Leps and Smilauer 2003). To analyse if the seasons are significantly different from each other I again conducted a one-way ANOVA with a Tukey HSD posthoc test (SPSS 15.0; independent variables: axis scores of the DCA; dependent variable: season).

To investigate the dietary overlap of chamois and ibex, I used the ibex data collected and presented by Zingg (2009). To analyse whether the two species potentially compete for forage within the study area, the total number of fragments of *Cyperaceae*, *Poaceae*, herbs,

Ericaceae, unknown dicots, conifers and others (including ferns, mosses and unknown fragments) were $\log(x+1)$ transformed to fulfil the homogeneity and normality criteria and analysed by a one-way ANOVA with a Tukey HSD posthoc test. To investigate if there are relevant differences between the chamois forage and ibex forage during the four seasons, the plant species and groups contributing to more than 5% to the forage for either season or animals species, were $\log(x+1)$ transformed to fulfil the homogeneity and normality criteria and analysed by a DCA followed by a one-way ANOVA with a Tukey HSD posthoc test (independent variables: axis scores of the DCA; dependent variable: season).

Results

Of all the 16000 plant fragments analysed of both animals species (8000 fragments each), only 71 fragments from chamois and 66 fragments from ibex dung could not be identified to any taxonomic level. All other fragments could be assigned to one of the following groups: *Cyperaceae*, *Poaceae*, herbs, *Ericaceae*, unknown dicots, conifers, ferns and mosses, in some cases even to species level (see Table 2 and 3).

Composition of chamois forage over the course of a year

Graminoids (*Cyperaceae* and *Poaceae*) were the dominating forage items of chamois at all times of the year. The consumption of *Cyperaceae* decreased significantly from spring to summer and increased significantly from autumn to winter, but was not significantly different between winter and spring as well as summer and autumn ($F = 44.133$ $p < 0.001$; Table 2 and 3, Figure 5). The differences in *Poaceae* consumption were less distinct, but still significant ($F = 3.443$, $p = 0.021$); significant differences were only found between autumn and winter.

The fraction of herbs increased from less than 2% in winter up to 30.8% in summer and significantly differed over the course of the seasons ($F = 40.741$, $p < 0.001$). Conifers were most often consumed in winter and consumption decreased rapidly and significantly from spring to summer where it remained constant and did not significantly differ from the autumn consumption ($F = 50.773$, $p < 0.001$). The *Ericaceae* consumption was fairly low and only differed significantly between summer and autumn ($F = 3.243$, $p = 0.027$; Table 2 and 3, Figure 5).

Table 2: Number and % of fragments per plant species or group identified from faecal pellets of chamois and ibex collected during winter and spring 2008 in the SNP. The grand total results form the highlighted totals.

	Winter				Spring			
	Chamois		Ibex		Chamois		Ibex	
	Number	%	Number	%	Number	%	Number	%
<i>Carex sp.</i>	470	23.5	249	12.45	257	12.85	247	12.35
<i>Elyna myosuroides</i>	67	3.35	56	2.8	165	8.25	143	7.15
unknown <i>Cyperaceae</i>	141	7.05	51	2.55	77	3.85	30	1.5
total <i>Cyperaceae</i>	678	33.9	356	17.8	499	24.95	420	21
<i>Festuca ovina</i>	107	5.35	141	7.05	105	5.25	108	5.4
<i>Festuca rubra/F. violacea</i>	97	4.85	155	7.75	183	9.15	141	7.05
<i>Festuca sp.</i>	73	3.65	64	3.2	65	3.25	79	3.95
<i>Nardus stricta</i>	0	0	3	0.15	1	0.05	7	0.35
<i>Sesleria caerulea</i>	141	7.05	225	11.25	236	11.8	176	8.8
group 1	53	2.65	58	2.9	61	3.05	27	1.35
group 2	49	2.45	117	5.85	52	2.6	86	4.3
group 3	59	2.95	103	5.15	44	2.2	74	3.7
unknown <i>Poaceae</i>	234	11.7	246	12.3	252	12.6	217	10.85
total <i>Poaceae</i>	813	40.65	1112	55.6	999	49.95	915	45.75
total graminoids	1491	74.55	1468	73.4	1498	74.9	1335	66.75
herbs	32	1.6	30	1.5	111	5.55	174	8.7
total herbs	32	1.6	30	1.5	111	5.55	174	8.7
<i>Erica carnea</i>	1	0.05	3	0.15	28	1.4	40	2
<i>Rhododendron sp.</i>	6	0.3	19	0.95	9	0.45	3	0.15
<i>Vaccinium myrtillus</i>	0	0	0	0	0	0	0	0
<i>Vaccinium vitis-idaea</i>	6	0.3	5	0.25	7	0.35	2	0.1
unknown <i>Ericaceae</i>	97	4.85	133	6.65	84	4.2	97	4.85
total <i>Ericaceae</i>	110	5.5	160	8	128	6.4	142	7.1
unknown dicots	110	5.5	162	8.1	95	4.75	170	8.5
total dicots	252	12.6	352	17.6	334	16.7	486	24.3
<i>Juniperus communis</i>	0	0	0	0	1	0.05	1	0.05
<i>Larix decidua</i>	151	7.55	59	2.95	66	3.3	89	4.45
<i>Picea abies</i>	12	0.6	3	0.15	9	0.45	6	0.3
<i>Pinus sp.</i>	73	3.65	52	2.6	71	3.55	22	1.1
unknown conifers	2	0.1	41	2.05	2	0.1	25	1.25
total conifers	238	11.9	155	7.75	149	7.45	143	7.15
ferns	0	0	6	0.3	0	0	0	0
mosses	1	0.05	8	0.4	3	0.15	8	0.4
unknown fragments	18	0.9	11	0.55	16	0.8	28	1.4
total others	19	0.95	25	1.25	19	0.95	36	1.8
total	2000	100	2000	100	2000	100	2000	100

group 1: *Agrostis capillaris/Anthoxanthum odoratum/Dactylis glomerata/Trisetum flavescens*, (*Briza media*)

group 2: *Deschampsia caespitosa/D. flexuosa/Phleum alpinum*, (*Helictotrichon pubescens*, *Briza media*)

group 3: *Poa pratensis*, (*Helictotrichon pubescens*)

Table 3: Number and % of fragments per plant species or group identified from faecal pellets of chamois and ibex collected during summer and autumn 2008 in the SNP. The grand total results form the highlighted totals.

	Summer				Autumn			
	Chamois		Ibex		Chamois		Ibex	
	Number	%	Number	%	Number	%	Number	%
<i>Carex sp.</i>	41	2.05	36	1.8	42	2.1	86	4.3
<i>Elyna myosuroides</i>	63	3.15	35	1.75	47	2.35	69	3.45
unknown <i>Cyperaceae</i>	56	2.8	19	0.95	28	1.4	30	1.5
total <i>Cyperaceae</i>	160	8	90	4.5	117	5.85	185	9.25
<i>Festuca ovina</i>	40	2	79	3.95	146	7.3	194	9.7
<i>Festuca rubra/F. violacea</i>	112	5.6	169	8.45	175	8.75	204	10.2
<i>Festuca sp.</i>	47	2.35	42	2.1	3	0.15	0	0
<i>Nardus stricta</i>	0	0	0	0	0	0	0	0
<i>Sesleria caerulea</i>	132	6.6	173	8.65	232	11.6	187	9.35
group 1	92	4.6	131	6.55	64	3.2	158	7.9
group 2	168	8.4	283	14.15	82	4.1	149	7.45
group 3	84	4.2	121	6.05	76	3.8	95	4.75
unknown <i>Poaceae</i>	374	18.7	207	10.35	389	19.45	288	14.4
total <i>Poaceae</i>	1049	52.45	1205	60.25	1167	58.35	1275	63.75
total graminoids	1209	60.45	1295	64.75	1284	64.2	1460	73
herbs	615	30.75	444	22.2	220	11	114	5.7
total herbs	615	30.75	444	22.2	220	11	114	5.7
<i>Erica carnea</i>	12	0.6	0	0	20	1	25	1.25
<i>Rhododendron sp.</i>	2	0.1	5	0.25	32	1.6	15	0.75
<i>Vaccinium myrtillus</i>	0	0	0	0	4	0.2	0	0
<i>Vaccinium vitis-idaea</i>	0	0	5	0.25	0	0	7	0.35
unknown <i>Ericaceae</i>	25	1.25	98	4.9	180	9	169	8.45
total <i>Ericaceae</i>	39	1.95	108	5.4	236	11.8	216	10.8
unknown dicots	114	5.7	126	6.3	219	10.95	100	5
total dicots	768	38.4	678	33.9	675	33.75	430	21.5
<i>Juniperus communis</i>	2	0.1	0	0	0	0	1	0.05
<i>Larix decidua</i>	5	0.25	1	0.05	5	0.25	42	2.1
<i>Picea abies</i>	1	0.05	0	0	1	0.05	0	0
<i>Pinus sp.</i>	1	0.05	1	0.05	2	0.1	42	2.1
unknown conifers	0	0	0	0	0	0	1	0.05
total conifers	9	0.45	2	0.1	8	0.4	86	4.3
ferns	0	0	0	0	0	0	1	0.05
mosses	3	0.15	18	0.9	7	0.35	5	0.25
unknown fragments	11	0.55	7	0.35	26	1.3	18	0.9
total others	14	0.7	25	1.25	33	1.65	24	1.2
total	2000	100	2000	100	2000	100	2000	100

group 1: *Agrostis capillaris/Anthoxanthum odoratum/Dactylis glomerata/Trisetum flavescens, (Briza media)*

group 2: *Deschampsia caespitosa/D. flexuosa/Phleum alpinum, (Helictotrichon pubescens, Briza media)*

group 3: *Poa pratensis, (Helictotrichon pubescens)*

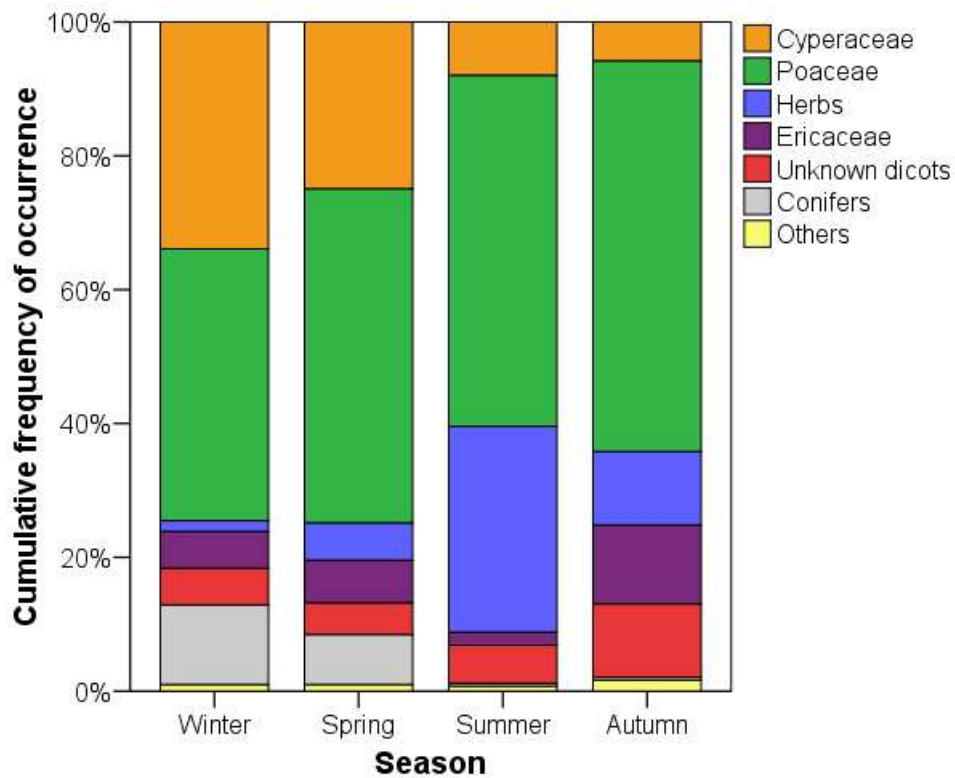


Figure 5: Cumulative frequency of forage composition of chamois in winter, spring, summer and autumn according to Table 2 and Table 3.

The DCA explained 52.2% of the variance in chamois forage composition on the first two axes (axis 1: 38.1%, axis 2: 14.1%) and again, a seasonal variation can clearly be seen (Figure 6): On axis 1 the winter samples have the lowest scores and are characterized by high fractions of conifers (Figure 7) and the summer samples received the highest scores (Figure 6) and are characterized by herbs as well as group 2 fragments (Figure 7). Spring and autumn samples are located between these two extremes with a closer relation of spring to winter and autumn to summer samples (Figure 6). However, consumption patterns were significantly different among all four seasons on axis 1 ($F = 80.607$, $p < 0.001$; Figure 8). Even though the one-way ANOVA with a Tukey HSD posthoc test was also significant for axis 2 ($F = 3.704$, $p = 0.015$), the only significant difference was found between autumn and winter but not between the other seasons (Figure 9). The variation shown on axis 2 seems to be mainly caused by differences between individual samples and not by seasonal variability

(Figure 5) and differences in the forage composition of individual chamois seem to be larger in autumn and winter compared to spring and summer.

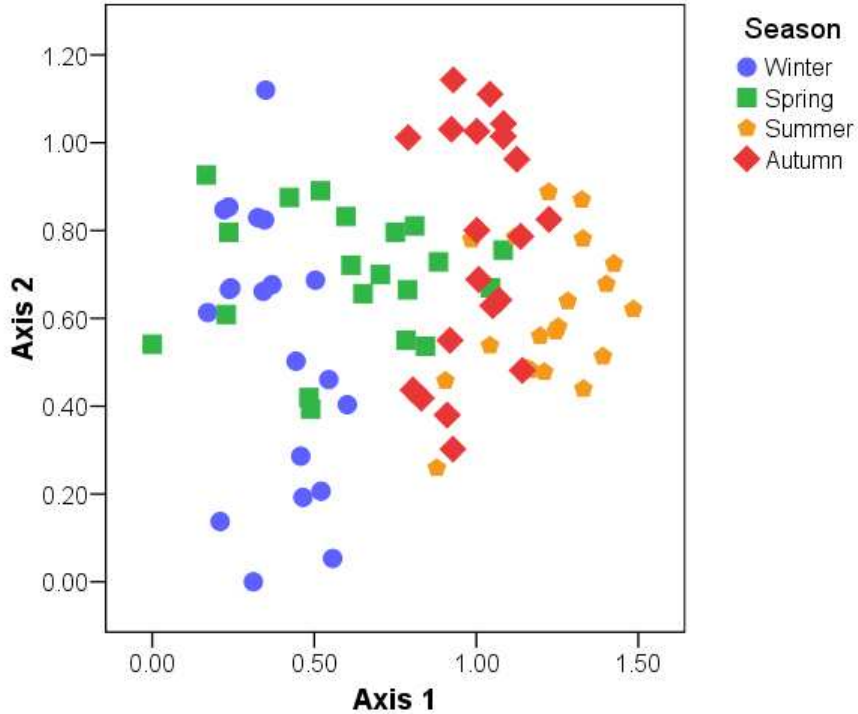


Figure 6: DCA of the chamois forage samples.

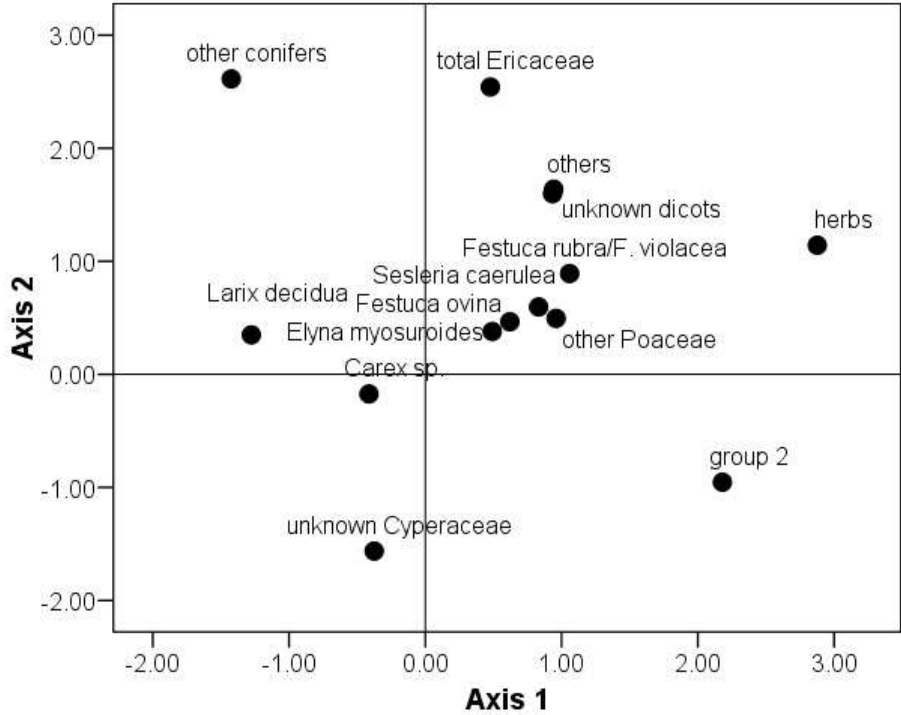


Figure 7: DCA of the plant species and groups found in chamois forage.

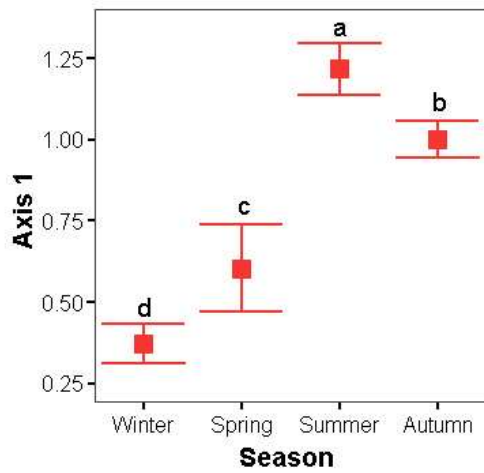


Figure 8: Mean scores of DCA of axis 1 for chamois forage composition. The bars represent the standard error (95% confidence interval) and the different letters indicate significantly different mean axis scores (significance level $\alpha = 0.05$, $n = 20$ for each season).

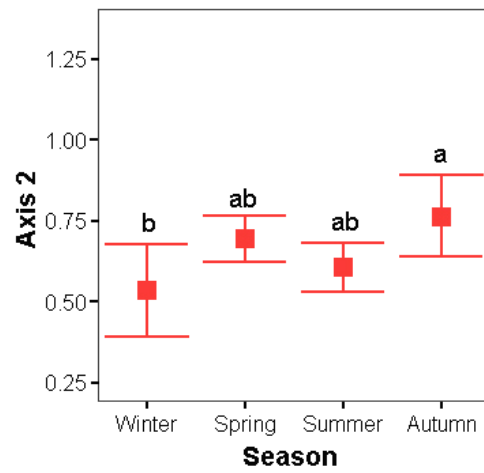


Figure 9: Mean scores of DCA of axis 2 for chamois forage composition. The bars represent the standard error (95% confidence interval) and the different letters indicate significantly different mean axis scores (significance level $\alpha = 0.05$, $n = 20$ for each season).

Feeding interactions between chamois and ibex

Looking at the total amount of consumed *Cyperaceae*, *Poaceae*, herbs, *Ericaceae* and conifer fragments of chamois and ibex, the differences are quite small: chamois and ibex forage composition only differed significantly with respect to *Cyperaceae* ($F = 33.742$, $p < 0.001$) and *Ericaceae* ($F = 4.315$, $p < 0.001$) in summer, *Poaceae* in winter ($F = 4.877$, $p < 0.001$) and conifers in autumn ($F = 27.819$, $p < 0.001$; Table 2 and 3; Figure 10).

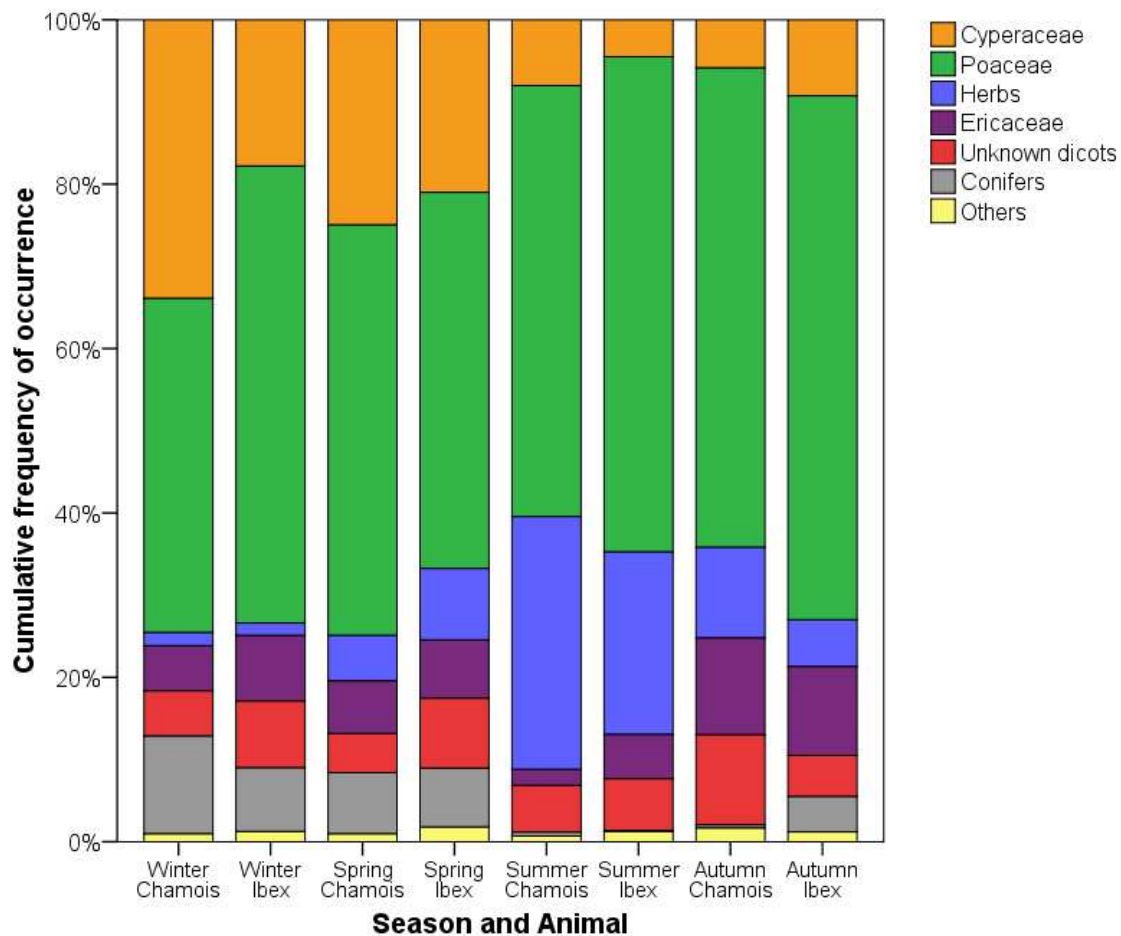


Figure 10: Cumulative frequency of chamois and ibex forage composition in winter, spring, summer and autumn according to Table 2 and Table 3.

The DCA for the chamois and ibex data explained 46.3% of the variance on the first two axes (axis 1: 32.3%, axis 2: 14.0%). An overlap of consumed forage items can be observed in spring, summer and autumn (Figure 11), but not in winter, where chamois and ibex samples were found to contain different forage items. Again, the first axis separates the seasons, with the most negative values representing the winter samples. The summer samples received the highest scores on axis 1; spring and autumn samples are located between these two extremes with a closer relation of spring to winter and autumn to summer samples (Figure 11). In Figure 12 the separation among the plant species and groups can be observed on axis 1: the conifers are having the most negative, the herbs the most positive

axis scores and in-between *Cyperaceae*, *Poaceae* and *Ericaceae* classes are found. The composition of the chamois and ibex forage only differed significantly from one another during winter, but not during the other seasons ($F = 63.579$, $p < 0.001$, Figure 13). Even though the one-way ANOVA with a Tukey HSD posthoc test was significant for axis 2 ($F = 2.176$, $p = 0.039$) this axis did not explain any variation in the composition of forage consumed at different times of the year (Figure 14).

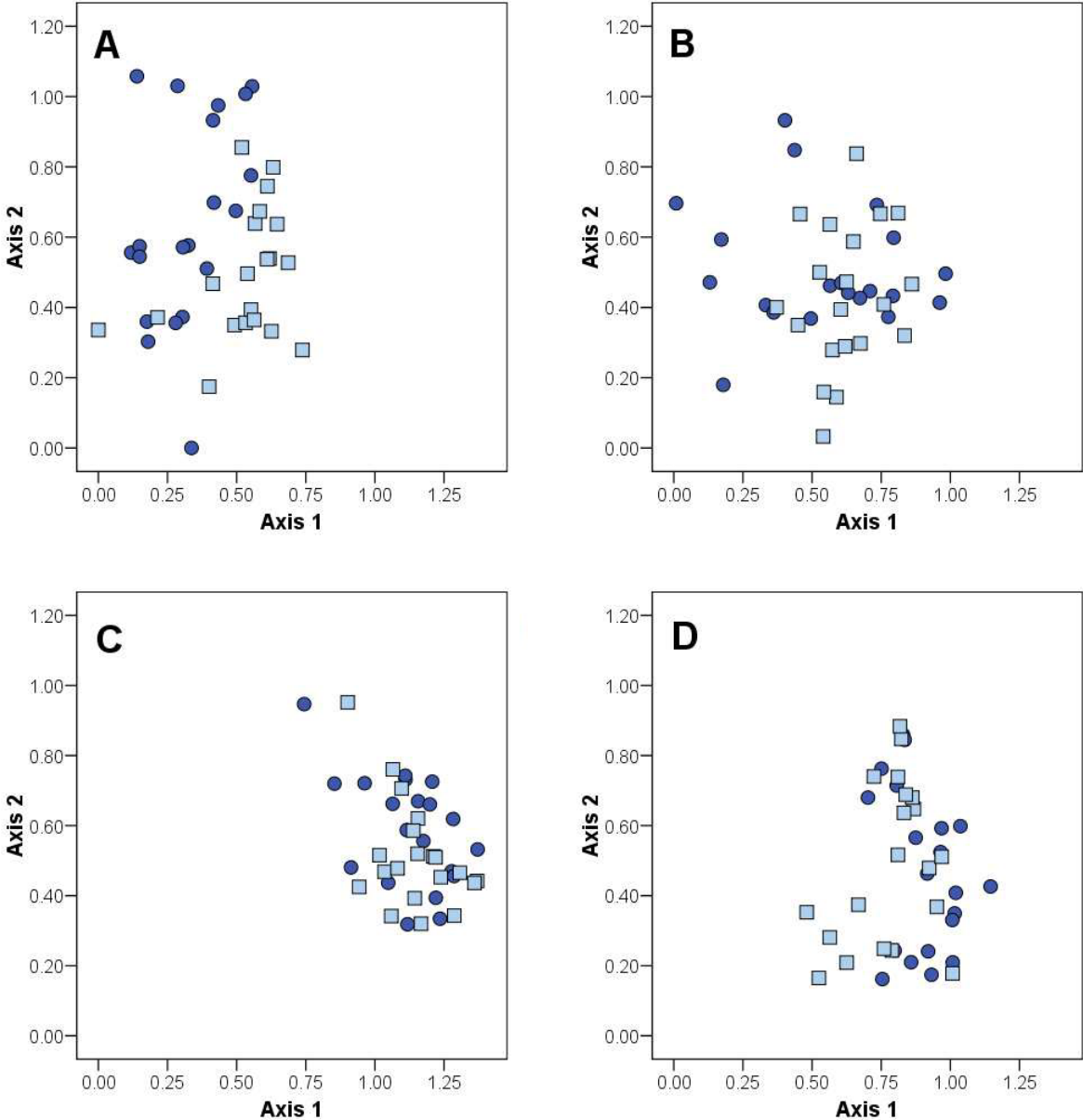


Figure 11: DCA of the chamois and ibex forage samples in A) winter, B) spring, C) summer and D) autumn. Chamois = circles, ibex = squares.

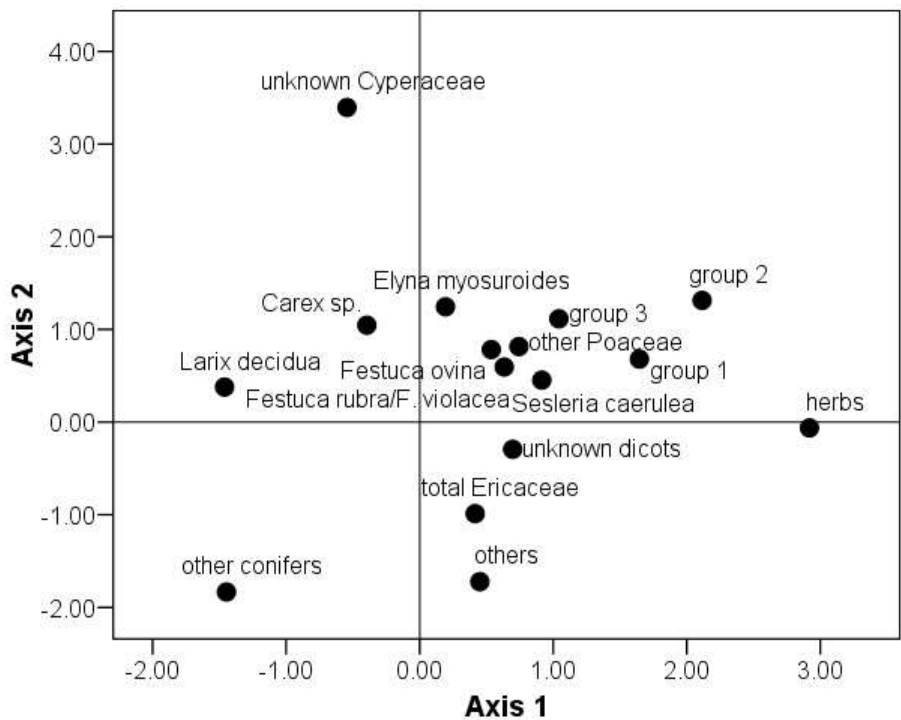


Figure 12: DCA of the plant species and groups found in chamois and ibex forages.

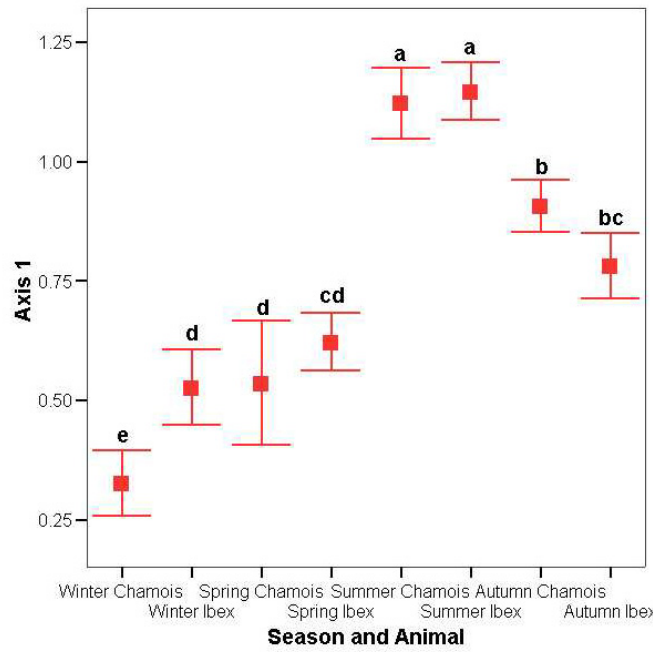


Figure 13: Mean scores of DCA axis 1 for chamois and ibex forage composition. The bars represent the standard error (95% confidence interval) and the different letters indicate significantly different mean axis scores (significance level alpha = 0.05, n = 20 for each animal species and season).

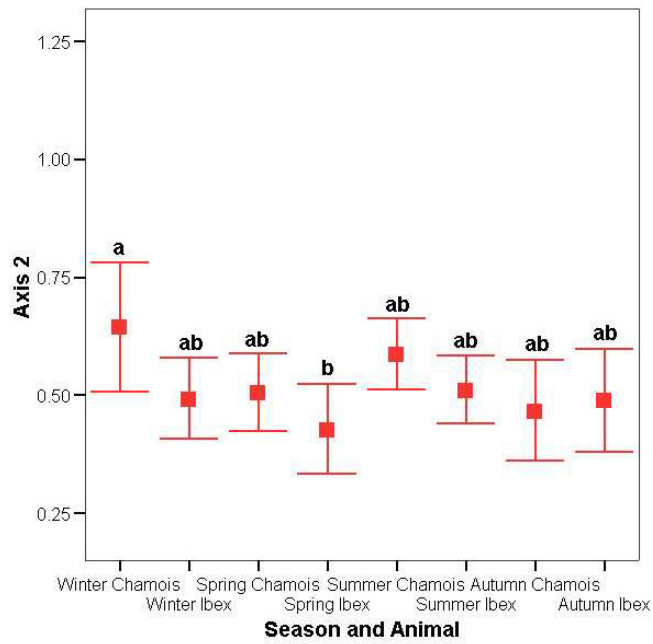


Figure 14: Mean scores of DCA axis 2 for chamois and ibex forage composition. The bars represent the standard error (95% confidence interval) and the different letters indicate significantly different mean axis scores (significance level $\alpha = 0.05$, $n = 20$ for each animal species and season).

Discussion

Forage composition and seasonality

In this study I assessed the seasonal variability in the composition of chamois forage based on epidermal fragment analysis of dung samples and compared the results with the ones obtained from the alpine ibex. This comparison allowed addressing whether forage competition might occur between these two species.

Overall, my results showed that many of the graminoids consumed belong to species that are known to be preferred by chamois (Baumann 2004, Garcia-Gonzalez and Cuartas 1996): *Sesleria caerulea*, different *Festuca* species, *Anthoxanthum odoratum*, *Dactylis glomerata*, *Phleum alpinum* and *Poa alpina*. Also the relatively high amount of *Cyperaceae* fragments I detected in winter is not unusual since *Carex sempervirens* and *Elyna myosuroides* are known to be frequently consumed during this season (Baumann 2004). Nevertheless, more important than certain forage species, likely is the possibility to feed on green and young plant items (Baumann 2004).

Regardless of the seasons, graminoids were the most frequently consumed plant species in my study area, with values ranging from 60 to 75%. These numbers are similar to the ones of the faecal analysis of Garcia-Gonzalez and Cuartas (1996), who found between 49 and 66% graminoids in the forage of the Pyrenean chamois collected from the Ordesa National Park in Spain over the course of a year. In contrast, Hegg (1961), whose faecal analysis was also conducted in the Swiss National Park, reported only about 30% graminoids. Baumann (2004) declares graminoid ratios of much more than 50% are even possible in summer; however, it is not clear how these results were obtained. Moreover, 90% graminoids in summer and 60% in winter have been found by botanical rumen analysis in Schröder (1977) for the chamois in the Ammgauer Mountains, Germany.

Similarly to chamois, also alpine ibex most frequently consumed graminoids in the SNP. These findings are similar to the observation data of Ten Houte de Lange (1978), who found that ibex at Piz Albris, Upper Engadine, Switzerland consumed 60% graminoids.

Klansek et al. (1995) who investigated the rumen contents of ibex in the Albris colony reported a graminoid consumption of almost 90% in summer and 85% in winter. Schröder and Kofler (1984) in contrast found only 5% graminoids and about 70% conifers in the ibex rumen in the Hochlantsch Mountains, Austria in winter. In the investigations of Klansek et al. (1995) the fraction of herbs in the ibex rumens made up about 1% in winter and 6% in summer, which is quite low compared to the herb consumption of the ibex in the valleys of Trupchun and Müschauns. For the chamois, Hegg (1961) reported a much higher herb (summer 55%; winter 15%) and *Ericaceae* amount (summer 25%; winter 10%) compared to my study.

Recently much effort has been given to classify ruminants into three feeding types based on their mouth morphology and digestive physiology, as well as their body size, feeding habit, activity times and phylogeny (Hoffmann 1989, Mysterud 1998, Mysterud et al. 2001, Perez-Barberia et al. 2001, Janis 2008). Browsers are those animals that selectively feed on nutrient rich plant material, grazers are those which mainly feed on graminoids and finally, intermediates are those species which feed on a mixture of the two plant types (Gordon 2003). However, the classification into these feeding types is not consistent in the literature since some publications use a threshold of >75% of the respective forage to allocate a species to grazers or browsers, whereas others use a threshold of >90% (Clauss et al. 2008). While the ibex might be classified as mixed feeder (Pérez-Barbería et al. 2001) with some grazer features (Hoffmann 1989) or as grazer with some mixed feeder aspects (Klansek et al. 1995), it is quite undoubted that chamois belong to the mixed feeder class. It is also reported that chamois are having a preference for forage plants with higher digestibility and higher energy content than the ibex (Raillard 1985, Leoni 1985). This preference likely results from the smaller body size of chamois. This species therefore needs to consume comparatively high-quality forage, whereas the ibex as bigger animal species should be able to satisfy its need on abundant and low-quality forage (Raillard 1985, Leoni 1985). However, since the differences in forage compositions were only small between chamois and ibex in my study, I could not confirm these findings.

Competition and Coexistence

To allow coexistence between competitors, sufficient differences in their ecological niches are essential. They can achieve these by consuming different forage or by inhabiting different ranges (Schoener 1982). In the Alps, chamois and ibex usually inhabit different habitats – in particular in winter – which might explain their successful coexistence. According to this, ibex are found at slightly higher elevations compared to chamois (Shackleton et al. 1997). In addition, ibex are known to prefer open habitats (Pérez-Barbería et al. 2001) with southerly exposed steep and rocky areas (Nievergelt and Zingg 1986, Abderhalden 2005). Chamois, in contrast, have a preference for a mixture of open and closed habitats (Pérez-Barbería et al. 2001) and stay on meadows or migrate into the forest in winter (Sägesser and Krapp 1986). However, in my study area, long-term observations of the park administration showed that both ibex and chamois inhabit more or less the same habitat (also cf. Figures 3 and 4).

My results showed significant differences in forage composition of these two species only in winter, but not during the other seasons. These findings indicate that in times when plenty of forage is available, chamois and ibex feed on the same forage, whereas in winter, when forage is scarce and competition occurs, resource partitioning, seem to happen (Gordon and Illius 1989). But having a closer look at the population fluctuations of both species (Figure 2) it is strikingly that both populations increase and decrease more or less simultaneously over time. Even though interspecific competition seem to occur between chamois and ibex in winter, obviously it is not strong enough to influence the population dynamics of these two species. Therefore, environmental factors such as weather and climate are probably more important. Since temperature, snow cover and rainfall are known to influence plants growth and consequently the biomass and the nutritive value of forage, annual variation of these factors might significantly influence fecundity, growth and survival of both species (Klein 1965, Langvatn et al. 1996, Post and Stenseth 1999, Coulson et al. 2001, Forchhammer et al. 2001, Sims et al. 2007, Grotan et al 2008). However, to fully understand the factors influencing the population dynamics of chamois and ibex in the

valleys of Trupchun and Müschauns, further investigations have to be conducted. Additionally, it would be interesting to enlarge this study with the third ungulate species, the red deer, to investigate its role in this community.

Acknowledgements

I specially thank Annatina Zingg for providing the ibex data. I also thank Dr. Anita C. Risch and Dr. Martin Schütz for supporting my master thesis in many different ways. Also thanks go to the Swiss National Park administration for help with the collection of samples and providing me with additional data. I also thank Pr. Dr. Heinz-Ulrich Reyer for accepting me as Master student.

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Figures

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http://images.google.ch/imgres?imgurl=http://www.dav-felsinfo.de/html/media/27/steinbock_npberchtesgaden.jpg&imgrefurl=http://www.dav-felsinfo.de/html/index.php%3Foption%3Dcom_content%26task%3Dview%26id%3D347%26Itemid%3D156&usg=__uglQ8UD4PqLseYrBPeitqTIXHEk=&h=220&w=171&sz=15&hl=de&start=4&tbnid=2PyEqmOhxMT6MM:&tbnh=107&tbnw=83&prev=/images%3Fq%3DSteinbock%2BBerchtesgaden%26gbv%3D2%26hl%3Dde%26sa%3DX, 9.2.2009

Figure 1

Niethammer J, Krapp F (eds) (1986) Bovidae Gray, 1821 - Hornträger, Rinder. In: Handbuch
der Säugetiere Europas - Band 2 Paarhufer. AULA Verlag, Wiesbaden, pp 269-277

Figure 2

unpublished data. Swiss National Park, Zernez

Figure 3

Haller, R (2006) Die räumliche Verteilung der Huftiere im Schweizerischen Nationalpark - Evaluation der Aufnahme- und Analysemethoden und Vergleich mit den Bestandserhebungen. In: Filli, F, Suter W (eds.): Huftierforschung im Schweizerischen Nationalpark. Nationalpark-Forschung in der Schweiz 93. Swiss Academy of Science, Bern, pp 45-78

Figure 4

Haller, R (2006) Die räumliche Verteilung der Huftiere im Schweizerischen Nationalpark - Evaluation der Aufnahme- und Analysemethoden und Vergleich mit den Bestandserhebungen. In: Filli, F, Suter W (eds.): Huftierforschung im Schweizerischen Nationalpark. Nationalpark-Forschung in der Schweiz 93. Swiss Academy of Science, Bern, pp 45-78

Appendix

Table A 1: Raw data: Number of fragments of plant species or groups identified in the 20 faecal samples of chamois in winter in the SNP.

	Winter chamois samples																				Total
	ch1	ch2	ch3	ch4	ch5	ch6	ch7	ch8	ch9	ch10	ch11	ch12	ch13	ch14	ch15	ch16	ch17	ch18	ch19	ch20	
<i>Carex</i> sp.	40	33	25	35	31	20	18	36	25	14	18	9	21	23	17	26	10	12	35	22	470
<i>Elyna myosuroides</i>	0	0	1	1	8	6	6	6	2	6	12	3	1	1	1	2	0	6	1	4	67
unknown Cyperaceae	8	7	7	16	17	8	8	10	10	8	6	4	4	1	6	6	0	2	6	7	141
<i>Festuca ovina</i>	5	7	11	2	0	2	9	6	2	4	6	2	5	4	1	13	9	4	11	4	107
<i>Festuca rubra</i> /F. violacea	4	2	1	0	1	2	13	2	4	4	1	13	8	6	10	4	5	7	8	2	97
<i>Festuca</i> sp.	1	3	1	6	3	2	2	2	8	4	3	4	4	5	4	6	1	1	5	8	73
<i>Nardus stricta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sesleria caerulea</i>	11	6	7	1	2	8	4	2	2	4	9	19	6	9	8	19	4	13	2	5	141
group 1	1	5	1	2	1	4	2	2	3	0	4	3	2	1	3	1	6	5	6	1	53
group 2	2	13	1	8	3	1	0	6	2	2	0	5	0	2	0	0	1	0	3	0	49
group 3	6	2	3	3	1	15	4	2	2	2	2	7	5	3	1	0	0	0	0	0	59
unknown Poaceae	14	17	9	12	14	24	14	15	21	9	10	15	8	5	5	6	8	7	8	13	234
herbs	1	0	0	0	0	3	2	0	6	9	3	0	2	1	1	0	2	1	1	0	32
<i>Erica carnea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Rhododendron</i> sp.	0	0	0	0	0	0	0	1	0	1	0	0	2	0	1	0	0	0	0	1	6
<i>Vaccinium myrtilloides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium vitis-idaea</i>	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	6
unknown Ericaceae	0	0	5	0	2	0	5	5	2	11	7	1	8	13	8	5	7	3	4	11	97
unknown dicots	3	3	8	2	2	1	4	3	5	8	4	7	7	8	8	5	7	12	5	8	110
<i>Juniperus communis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Larix decidua</i>	4	2	15	10	15	4	4	2	5	10	11	5	9	11	13	2	3	13	3	10	151
<i>Picea abies</i>	0	0	0	0	0	0	2	0	0	1	0	1	1	3	1	0	1	1	0	1	12
<i>Pinus</i> sp.	0	0	4	0	0	0	2	0	0	2	2	2	2	4	7	5	32	11	0	0	73
unknown conifers	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2
ferns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
mosses	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
unknown fragments	0	0	1	2	0	0	1	0	1	1	1	0	3	0	4	0	1	0	1	2	18

group 1: *Agrostis capillaris*/*Anthoxanthum odoratum*/*Dactylis glomerata*/*Trisetum flavescens*, (*Briza media*)

group 2: *Deschampsia caespitosa*/*D. flexuosa*/*Phleum alpinum*, (*Helictotrichon pubescens*, *Briza media*)

group 3: *Poa pratensis*, (*Helictotrichon pubescens*)

Table A 2: Raw data: Number of fragments of plant species or groups identified in the 20 faecal samples of chamois in spring in the SNP.

	Spring chamois samples																				Total
	ch21	ch22	ch23	ch24	ch25	ch26	ch27	ch28	ch29	ch30	ch31	ch32	ch33	ch34	ch35	ch36	ch37	ch38	ch39	ch40	
Carex sp.	12	32	5	9	18	39	12	8	14	18	27	20	11	2	0	11	7	4	5	3	257
Elyna myosuroides	8	2	0	2	5	2	4	15	10	10	3	10	24	10	19	10	8	3	8	12	165
unknown Cyperaceae	0	1	0	0	0	0	0	2	0	0	11	13	11	6	2	12	11	4	4	0	77
Festuca ovina	9	6	13	8	7	4	9	11	6	4	8	4	3	4	1	2	1	0	1	4	105
Festuca rubra/F. violacea	8	14	13	17	6	3	13	7	10	15	9	1	9	5	14	4	5	12	9	9	183
Festuca sp.	4	2	5	4	2	1	4	0	8	6	7	1	1	2	3	5	2	4	1	3	65
Nardus stricta	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sesleria caerulea	10	7	13	30	10	3	10	6	6	11	10	7	15	4	20	7	18	20	16	13	236
group 1	7	2	4	3	6	4	10	4	2	2	2	0	1	2	0	1	2	1	6	2	61
group 2	8	3	7	2	5	1	3	2	5	3	2	0	1	0	0	2	0	2	1	5	52
group 3	1	1	0	0	0	1	1	2	3	0	2	1	3	0	2	6	7	1	12	1	44
unknown Poaceae	11	8	19	13	19	12	15	14	21	12	11	5	13	11	10	10	7	11	12	18	252
herbs	11	6	12	6	6	0	7	6	4	11	0	1	0	5	1	0	0	6	13	16	111
Erica carnea	0	3	0	0	0	0	0	2	0	0	0	10	3	2	0	0	0	2	0	6	28
Rhododendron sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	8	0	0	0	0	0	0	9
Vaccinium myrtilloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium vitis-idaea	0	0	0	0	0	0	0	3	0	2	0	0	0	0	2	0	0	0	0	0	7
unknown Ericaceae	0	5	2	0	1	9	4	4	4	2	4	11	1	5	11	11	0	7	1	2	84
unknown dicots	6	3	4	2	7	0	4	9	1	2	3	1	3	19	4	1	1	13	6	6	95
Juniperus communis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Larix decidua	3	2	1	1	5	3	0	0	2	0	0	0	1	10	8	10	12	4	4	0	66
Picea abies	0	1	0	2	2	0	2	0	0	0	0	1	0	0	0	0	1	0	0	0	9
Pinus sp.	1	2	0	0	1	15	0	2	2	1	1	13	0	5	1	6	17	4	0	0	71
unknown conifers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2
ferns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
mosses	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	3
unknown fragments	0	0	2	1	0	2	0	3	2	1	0	1	0	0	1	2	0	0	1	0	16

group 1: *Agrostis capillaris*/*Anthoxanthum odoratum*/*Dactylis glomerata*/*Trisetum flavescens*, (*Briza media*)

group 2: *Deschampsia caespitosa*/*D. flexuosa*/*Phleum alpinum*, (*Helictotrichon pubescens*, *Briza media*)

group 3: *Poa pratensis*, (*Helictotrichon pubescens*)

Table A 3: Raw data: Number of fragments of plant species or groups identified in the 20 faecal samples of chamois in summer in the SNP.

	Summer chamois samples																				Total
	ch41	ch42	ch43	ch44	ch45	ch46	ch47	ch48	ch49	ch50	ch51	ch52	ch53	ch54	ch55	ch56	ch57	ch58	ch59	ch60	
Carex sp.	0	0	4	3	1	2	1	4	8	4	10	1	0	1	0	2	0	0	0	0	41
Elyna myosuroides	5	1	2	5	1	5	0	6	3	5	8	6	4	2	2	1	2	1	3	1	63
unknown Cyperaceae	3	1	0	2	1	6	6	0	5	0	25	4	0	0	0	0	2	0	1	0	56
Festuca ovina	3	5	1	0	4	0	5	3	1	3	3	1	2	1	3	0	0	3	0	2	40
Festuca rubra/F. violacea	11	2	7	5	14	6	4	7	7	6	2	3	5	3	4	1	10	4	4	10	112
Festuca sp.	2	3	1	1	7	0	2	5	2	5	2	2	5	0	0	2	2	4	2	0	47
Nardus stricta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sesleria caerulea	5	2	7	9	7	11	8	9	4	12	6	4	6	7	9	3	11	6	3	3	132
group 1	4	11	5	3	13	3	7	5	3	4	0	5	5	2	4	7	3	1	5	2	92
group 2	7	9	2	6	4	4	11	9	13	16	3	4	10	5	11	3	14	10	9	18	168
group 3	1	7	10	2	3	3	6	8	6	0	2	0	3	5	1	2	9	8	7	1	84
unknown Poaceae	8	26	11	20	14	11	17	33	12	21	14	14	18	16	28	17	26	18	24	26	374
herbs	38	29	39	35	29	40	26	11	28	19	20	29	37	43	27	40	19	39	35	32	615
Erica carnea	1	0	2	0	2	0	0	0	2	2	0	0	1	0	0	0	1	0	0	1	12
Rhododendron sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
Vaccinium myrtilloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium vitis-idaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
unknown Ericaceae	0	0	0	0	0	3	4	0	0	0	0	6	0	3	5	2	0	0	2	0	25
unknown dicots	12	2	7	9	0	5	3	2	3	3	3	19	2	10	5	19	0	3	3	4	114
Juniperus communis	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	2
Larix decidua	0	0	1	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	1	0	5
Picea abies	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Pinus sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
unknown conifers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ferns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
mosses	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	3
unknown fragments	0	2	1	0	0	0	0	1	0	0	2	0	1	0	1	0	1	1	1	0	11

group 1: *Agrostis capillaris*/*Anthoxanthum odoratum*/*Dactylis glomerata*/*Trisetum flavescens*, (*Briza media*)

group 2: *Deschampsia caespitosa*/*D. flexuosa*/*Phleum alpinum*, (*Helictotrichon pubescens*, *Briza media*)

group 3: *Poa pratensis*, (*Helictotrichon pubescens*)

Table A 4: Raw data: Number of fragments of plant species or groups identified in the 20 faecal samples of chamois in autumn in the SNP.

	Autumn chamois samples																				Total
	ch61	ch62	ch63	ch64	ch65	ch66	ch67	ch68	ch69	ch70	ch71	ch72	ch73	ch74	ch75	ch76	ch77	ch78	ch79	ch80	
Carex sp.	1	1	3	1	7	4	2	0	5	0	2	4	0	1	0	1	0	4	1	5	42
Elyna myosuroides	2	6	3	7	2	0	3	4	2	1	0	3	3	1	0	2	1	3	0	4	47
unknown Cyperaceae	1	2	0	3	7	1	1	2	0	2	0	0	2	1	1	0	0	0	1	4	28
Festuca ovina	12	7	5	6	9	1	7	2	3	26	4	8	20	1	8	7	5	5	0	10	146
Festuca rubra/F. violacea	10	12	10	13	7	2	13	2	6	16	8	13	13	5	4	5	10	12	5	9	175
Festuca sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	3
Nardus stricta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sesleria caerulea	12	12	17	6	8	1	18	2	8	22	8	26	15	10	8	4	8	17	8	22	232
group 1	1	3	1	6	2	6	0	3	0	3	3	4	1	3	9	5	2	3	6	3	64
group 2	11	7	5	3	5	4	3	1	1	5	0	2	3	1	3	3	2	12	0	11	82
group 3	3	3	7	0	9	8	10	3	3	3	6	1	6	2	3	3	3	1	1	1	76
unknown Poaceae	41	23	12	7	30	17	25	17	13	19	12	26	32	8	23	9	9	32	11	23	389
herbs	1	13	22	14	6	6	7	28	6	0	4	10	1	20	25	4	4	8	38	3	220
Erica carnea	0	0	0	7	0	0	0	0	7	0	2	0	0	4	0	0	0	0	0	0	20
Rhododendron sp.	0	0	0	0	0	31	0	1	0	0	0	0	0	0	0	0	0	0	0	0	32
Vaccinium myrtilloides	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	3	0	0	0	0	4
Vaccinium vitis-idaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
unknown Ericaceae	0	5	4	10	1	2	2	12	29	0	18	1	2	24	5	24	33	0	8	0	180
unknown dicots	1	5	9	16	4	6	7	21	16	3	32	0	1	19	9	28	21	1	18	2	219
Juniperus communis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larix decidua	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	5
Picea abies	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pinus sp.	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
unknown conifers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ferns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
mosses	0	0	1	0	0	5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	7
unknown fragments	1	1	1	1	2	3	1	2	0	0	1	2	1	0	1	2	2	2	2	1	26

group 1: *Agrostis capillaris*/*Anthoxanthum odoratum*/*Dactylis glomerata*/*Trisetum flavescens*, (*Briza media*)

group 2: *Deschampsia caespitosa*/*D. flexuosa*/*Phleum alpinum*, (*Helictotrichon pubescens*, *Briza media*)

group 3: *Poa pratensis*, (*Helictotrichon pubescens*)

Table A 5: Raw data: Number of fragments of plant species or groups identified in the 20 faecal samples of ibex in winter in the SNP.

	Winter ibex samples																				Total
	ib1	ib2	ib3	ib4	ib5	ib6	ib7	ib8	ib9	ib10	ib11	ib12	ib13	ib14	ib15	ib16	ib17	ib18	ib19	ib20	
Carex sp.	15	11	21	19	16	4	13	10	7	5	12	5	16	14	16	3	22	16	12	12	249
Elyna myosuroides	4	0	4	2	3	4	6	3	1	1	4	1	4	2	3	0	3	4	4	3	56
unknown Cyperaceae	4	1	9	0	5	4	2	5	2	1	5	0	4	0	0	0	2	1	4	2	51
Festuca ovina	4	8	5	4	5	7	7	12	5	5	6	7	8	11	12	4	10	4	13	4	141
Festuca rubra/F. violacea	1	7	2	6	4	13	16	8	14	14	8	8	9	9	7	9	1	9	4	6	155
Festuca sp.	1	2	0	3	0	4	7	0	4	6	2	2	3	1	3	7	9	5	1	4	64
Nardus stricta	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	3
Sesleria caerulea	5	18	2	7	9	15	12	11	17	17	7	20	6	15	9	13	4	11	12	15	225
group 1	3	0	8	4	0	1	2	2	1	2	4	2	8	4	5	5	1	2	3	1	58
group 2	2	13	6	2	0	6	5	15	2	3	9	4	11	9	4	6	8	1	4	7	117
group 3	2	11	4	2	2	10	3	6	11	2	6	8	5	3	4	6	0	7	3	8	103
unknown Poaceae	4	13	22	7	10	15	5	14	6	10	19	7	19	8	14	22	15	14	14	8	246
herbs	2	0	1	2	0	1	2	0	2	2	0	3	0	0	0	5	2	4	2	2	30
Erica carnea	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	3
Rhododendron sp.	0	0	0	0	9	0	0	0	2	3	0	1	1	1	0	1	0	0	0	1	19
Vaccinium myrtilloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium vitis-idaea	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	2	5
unknown Ericaceae	13	4	9	6	2	4	9	2	9	18	1	12	0	11	8	4	0	6	9	6	133
unknown dicots	8	1	2	13	3	8	8	11	6	3	13	8	3	7	10	5	14	15	14	10	162
Juniperus communis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larix decidua	11	3	5	3	19	1	0	0	1	2	0	3	0	2	0	4	1	0	0	4	59
Picea abies	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3
Pinus sp.	18	3	0	18	1	3	0	0	2	3	0	2	1	0	1	0	0	0	0	0	52
unknown conifers	3	4	0	0	7	0	3	1	6	2	2	1	1	2	3	2	2	1	1	0	41
ferns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	1	6
mosses	0	0	0	1	3	0	0	0	0	0	0	0	0	0	1	2	0	0	0	1	8
unknown fragments	0	1	0	0	1	0	0	0	1	0	2	0	1	1	0	2	1	0	0	1	11

group 1: *Agrostis capillaris*/*Anthoxanthum odoratum*/*Dactylis glomerata*/*Trisetum flavescens*, (*Briza media*)

group 2: *Deschampsia caespitosa*/*D. flexuosa*/*Phleum alpinum*, (*Helictotrichon pubescens*, *Briza media*)

group 3: *Poa pratensis*, (*Helictotrichon pubescens*)

Table A 6: Raw data: Number of fragments of plant species or groups identified in the 20 faecal samples of ibex in spring in the SNP.

	Spring ibex samples																				Total
	ib21	ib22	ib23	ib24	ib25	ib26	ib27	ib28	ib29	ib30	ib31	ib32	ib33	ib34	ib35	ib36	ib37	ib38	ib39	ib40	
<i>Carex</i> sp.	8	21	23	7	12	5	11	3	9	12	7	14	15	17	16	10	15	4	17	21	247
<i>Elyna myosuroides</i>	3	5	1	6	11	3	6	5	11	13	5	9	8	9	8	16	1	11	12	0	143
unknown Cyperaceae	0	0	6	6	4	0	1	0	0	0	3	0	0	0	0	1	0	5	4	0	30
<i>Festuca ovina</i>	5	6	6	3	8	1	5	6	0	10	6	7	4	6	6	7	8	3	2	9	108
<i>Festuca rubra</i> /F. violacea	3	7	5	6	4	4	10	5	3	6	6	11	7	7	3	14	9	9	10	12	141
<i>Festuca</i> sp.	1	7	4	5	3	5	1	5	2	12	3	8	1	4	7	2	1	2	2	4	79
<i>Nardus stricta</i>	1	2	0	0	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	7
<i>Sesleria caerulea</i>	3	10	8	8	9	4	10	9	7	11	8	6	11	9	8	10	11	7	12	15	176
group 1	0	0	1	4	2	2	3	2	0	0	2	0	0	0	1	3	0	5	2	0	27
group 2	1	4	1	11	4	4	6	5	1	3	5	3	6	4	3	8	3	7	6	1	86
group 3	1	4	3	2	4	3	2	4	0	7	11	0	0	0	5	9	4	2	10	3	74
unknown Poaceae	5	13	10	15	4	16	15	15	2	13	15	12	7	13	11	12	10	8	11	10	217
herbs	25	2	4	7	4	8	15	13	24	3	5	5	7	9	13	1	9	15	1	4	174
<i>Erica carnea</i>	0	1	4	5	3	1	1	0	3	0	4	2	4	2	1	0	2	5	1	1	40
<i>Rhododendron</i> sp.	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	3
<i>Vaccinium myrtilloides</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vaccinium vitis-idaea</i>	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
unknown Ericaceae	4	4	9	2	11	9	0	4	11	2	1	7	8	6	5	0	4	5	0	5	97
unknown dicots	15	4	2	7	11	19	6	11	12	3	6	10	7	10	10	4	19	10	2	2	170
<i>Juniperus communis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<i>Larix decidua</i>	25	4	2	1	2	11	8	10	6	0	11	1	0	0	0	3	0	2	2	1	89
<i>Picea abies</i>	0	2	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	6
<i>Pinus</i> sp.	0	0	8	5	3	0	0	0	0	0	1	0	0	0	0	0	0	0	5	0	22
unknown conifers	0	2	1	0	0	4	0	0	3	3	0	1	6	2	0	0	0	0	0	3	25
ferns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
mosses	0	0	2	0	0	0	0	1	3	0	0	0	1	0	0	0	0	0	0	1	8
unknown fragments	0	2	0	0	1	0	0	1	3	1	0	3	2	1	1	0	4	0	1	8	28

group 1: *Agrostis capillaris*/*Anthoxanthum odoratum*/*Dactylis glomerata*/*Trisetum flavescens*, (*Briza media*)

group 2: *Deschampsia caespitosa*/*D. flexuosa*/*Phleum alpinum*, (*Helictotrichon pubescens*, *Briza media*)

group 3: *Poa pratensis*, (*Helictotrichon pubescens*)

Table A 7: Raw data: Number of fragments of plant species or groups identified in the 20 faecal samples of ibex in summer in the SNP.

	Summer ibex samples																				Total
	ib41	ib42	ib43	ib44	ib45	ib46	ib47	ib48	ib49	ib50	ib51	ib52	ib53	ib54	ib55	ib56	ib57	ib58	ib59	ib60	
Carex sp.	1	0	0	3	1	2	3	2	4	3	1	4	2	0	4	2	0	2	2	0	36
Elyna myosuroides	2	1	0	2	3	4	0	1	13	2	1	2	0	0	3	0	0	0	1	0	35
unknown Cyperaceae	1	1	0	1	1	2	0	0	9	0	0	1	0	0	2	1	0	0	0	0	19
Festuca ovina	3	2	6	7	7	1	8	8	3	3	8	3	3	4	0	3	2	4	1	3	79
Festuca rubra/F. violacea	6	3	8	12	11	9	8	9	12	7	7	15	11	7	8	10	5	8	5	8	169
Festuca sp.	4	1	3	3	1	4	3	2	1	2	4	1	3	1	1	1	2	2	2	1	42
Nardus stricta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sesleria caerulea	5	10	3	9	6	24	11	13	13	10	15	10	6	1	5	6	4	10	4	8	173
group 1	8	13	7	2	5	5	7	2	3	7	2	7	9	10	4	12	4	7	10	7	131
group 2	1	5	18	14	6	17	10	24	11	14	21	12	15	16	3	14	23	23	18	18	283
group 3	7	5	2	7	5	10	3	6	9	6	7	8	10	4	7	3	10	2	3	7	121
unknown Poaceae	8	7	8	15	9	6	13	15	9	12	17	7	12	12	6	10	10	13	8	10	207
herbs	37	32	36	22	17	12	25	14	11	25	11	12	19	29	30	20	24	18	26	24	444
Erica carnea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhododendron sp.	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	5
Vaccinium myrtilloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium vitis-idaea	2	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	5
unknown Ericaceae	5	9	6	2	3	2	4	2	2	6	4	5	5	4	16	7	4	3	5	4	98
unknown dicots	4	1	3	1	23	2	2	2	0	0	2	8	5	12	10	10	9	8	14	10	126
Juniperus communis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Larix decidua	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Picea abies	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinus sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
unknown conifers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ferns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
mosses	3	5	0	0	2	0	3	0	0	2	0	2	0	0	0	0	1	0	0	0	18
unknown fragments	2	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	7

group 1: *Agrostis capillaris*/*Anthoxanthum odoratum*/*Dactylis glomerata*/*Trisetum flavescens*, (*Briza media*)

group 2: *Deschampsia caespitosa*/*D. flexuosa*/*Phleum alpinum*, (*Helictotrichon pubescens*, *Briza media*)

group 3: *Poa pratensis*, (*Helictotrichon pubescens*)

Table A 8: Raw data: Number of fragments of plant species or groups identified in the 20 faecal samples of ibex in autumn in the SNP.

	Autumn ibex samples																				Total
	ib61	ib62	ib63	ib64	ib65	ib66	ib67	ib68	ib69	ib70	ib71	ib72	ib73	ib74	ib75	ib76	ib77	ib78	ib79	ib80	
Carex sp.	3	1	10	2	1	1	5	1	4	9	5	9	4	7	2	4	5	3	4	6	86
Elyna myosuroides	1	1	0	3	10	5	2	2	5	2	2	2	7	2	6	6	3	3	5	2	69
unknown Cyperaceae	0	0	3	0	0	1	1	0	1	5	6	0	1	1	4	3	0	1	2	1	30
Festuca ovina	10	4	5	1	6	4	4	2	17	26	11	15	16	2	17	18	10	5	12	9	194
Festuca rubra/F. violacea	9	4	10	12	7	8	13	11	13	12	13	11	10	8	14	13	8	9	14	5	204
Festuca sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nardus stricta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sesleria caerulea	7	5	14	14	12	2	4	12	16	13	12	13	6	4	9	7	7	14	8	8	187
group 1	17	14	4	8	10	6	6	7	3	9	9	8	10	4	9	7	4	8	5	10	158
group 2	3	5	2	1	3	5	3	2	3	5	15	14	6	6	9	11	17	4	12	23	149
group 3	4	6	7	5	6	5	5	1	6	5	8	2	4	1	6	5	7	4	2	6	95
unknown Poaceae	10	21	7	12	19	22	10	3	17	6	6	15	22	12	12	22	19	10	21	22	288
herbs	12	7	4	4	2	4	7	12	6	4	3	2	6	17	4	1	3	13	2	1	114
Erica carnea	0	7	1	3	0	2	7	3	0	0	1	0	0	1	0	0	0	0	0	0	25
Rhododendron sp.	2	0	0	3	0	6	0	0	0	0	0	0	0	2	0	0	2	0	0	0	15
Vaccinium myrtilloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium vitis-idaea	0	0	2	1	0	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	7
unknown Ericaceae	4	13	8	11	10	6	9	25	4	4	5	5	6	16	3	3	7	18	7	5	169
unknown dicots	10	1	7	3	6	4	8	16	5	0	3	2	1	13	1	0	6	8	5	1	100
Juniperus communis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Larix decidua	2	6	9	6	5	1	9	0	0	0	0	0	1	0	3	0	0	0	0	0	42
Picea abies	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pinus sp.	4	2	3	10	1	13	4	0	0	0	1	2	0	0	1	0	0	0	0	1	42
unknown conifers	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
ferns	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
mosses	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	5
unknown fragments	2	2	1	1	2	3	1	2	0	0	0	0	0	2	0	0	2	0	0	0	18

group 1: *Agrostis capillaris*/*Anthoxanthum odoratum*/*Dactylis glomerata*/*Trisetum flavescens*, (*Briza media*)

group 2: *Deschampsia caespitosa*/*D. flexuosa*/*Phleum alpinum*, (*Helictotrichon pubescens*, *Briza media*)

group 3: *Poa pratensis*, (*Helictotrichon pubescens*)