Seasonal variability in the diet composition of Alpine ibex (*Capra ibex ibex* L.) in the Swiss National Park

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Annatina Zingg

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Supervisors:
Dr. Anita C. Risch and Dr. Martin Schütz;
Community Ecology, Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Switzerland;
Prof. Dr. Heinz-Ulrich Reyer;
Institute of Zoology, University of Zurich, Switzerland

Zusammenfassung

Zu Beginn dieses Jahrhunderts haben verschiedene Populationen von Alpensteinböcken (*Capra ibex ibex* L.) in der Schweiz stark abgenommen. Bis zum jetzigen Zeitpunkt sind die Gründe dieser Abnahmen unklar. Nebst verschiedenen möglichen Ursachen wie genetischen, medizinischen oder Verhaltensfaktoren, könnte die Ressourcenverfügbarkeit einen grossen Einfluss auf die Populationsgrösse haben. Um zu verstehen, ob eine Tierpopulation in der Grösse durch limitierte Ressourcen beschränkt ist, ist es wichtig, Informationen über die Nahrungszusammensetzung im Verlaufe eines Jahres zu erhalten. Mit mikrohistologischen Analysen von Pflanzenfragmenten aus Kotproben habe ich quantitative Daten über die Nahrungszusammensetzung von Alpensteinböcken während vier Jahreszeiten im Schweizerischen National Park im Jahr 2008 gesammelt. Gramineen waren die dominierende Nahrung in allen Jahreszeiten, im Durchschnitt mit 69.5%, wobei keine signifikanten Unterschiede zwischen den Jahreszeiten beobachtet werden konnten. Allerdings, wenn die Monokoyledonen in *Cyperaceae* und *Poaceae* aufgetrennt wurden, konnten signifikante Unterschiede zwischen den Jahreszeiten festgestellt werden. Dicotyledonen waren die am zweithäufigsten konsumierte Pflanzengruppe mit 24.3%, gefolgt von 4.9% Koniferen und 1.4% anderen Pflanzenarten (Farne, Moose, unbestimmte Fragmente). Die Winter- und Frühlingsnahrung wurde durch den relativ hohen Anteil an Koniferen und *Cyperaceae* charakterisiert. Die Proben, welche im Sommer gesammelt wurden, unterschieden sich von den anderen durch den grossen Anteil an Kräutern, sowie den geringen Anteil an *Cyperaceae* und Koniferen. Die Herbstproben enthielten höhere Mengen an Fragmenten der Gattung *Festuca*. Mit den vorliegenden Daten erhalten wir einen relativ detaillierten Einblick in die Nahrungszusammensetzung des Alpensteinbocks im Jahresverlauf. Liegen einmal Daten über die Verfügbarkeit der Ressourcen im Gebiet vor, kann festgestellt werden, ob diese Ressourcen für die Steinbockpopulation limitierend wirken.

Abstract

At the beginning of this century several Swiss populations of Alpine ibex (*Capra ibex ibex* L.) decreased considerably, yet the reasons for these decreases are rather unclear. Among several different possibilities (genetic, medical or behavioural), resource availability could have a strong impact on the population size. To understand whether an animal population is constrained by limited resources, it is important to gain information on the diet composition over the course of the year. Using micro-histological analyses of plant fragments in faecal pellets I collected quantitative data on forage composition of Alpine ibex during four seasons in the Swiss National Park (SNP) in 2008. Graminoids were the dominant forage at all times of the year averaging 69.5% and did not significantly differ between the seasons. However, when separating the consumption of monocotyledons in *Cyperaceae* and *Poaceae,* significantly different frequencies were detected among the seasons. Dicotyledons were the second most frequently consumed group of plants with 24.3%, followed by 4.9% conifers and 1.4% other plant species (ferns, mosses, unidentified fragments). Winter and spring are characterized by the relatively high amount of conifers and *Cyperaceae*. The samples collected during summer were separated from the other samples by the high amount of herbs and low amount of conifers and *Cyperaceae*. The autumn samples contained higher amounts of *Festuca* species. Altogether, the present study provides detailed data on the diet composition of Alpine ibex over the course of the year, which will help to assess whether the population of these animals are resource limited once data on resource availability is collected.

Introduction

The population size of a large herbivore species can be influenced by a combination of stochastic and density-dependent factors (Framarin 1985, Cluttonbrock et al. 1991, Saether 1997, Gaillard et al. 1998, Gaillard et al. 2000, Saether et al. 2002). Density-dependent effects, mainly intraspecific competition for space and resources as well as the outbreak of diseases, emerge when population sizes are high and therefore the chance of survival constrains (Framarin 1985, Cluttonbrock et al. 1991). Similarly, climate variability can have large impacts on ungulate population dynamics (Saether et al. 1996, Gaillard et al. 2000, Mysterud 2000, Mysterud et al. 2001, Owen-Smith 2008). High variability in precipitation during the vegetation period generally alters the quality and/or quantity of forage plants (Post and Stenseth 1999), while high snow cover can constrain forage accessibility during winter (Post and Stenseth 1998, 1999, Owen-Smith 2008). As a result, individual fecundity, growth and survival of an animal can be affected (Saether et al. 1996, Saether 1997, Taillon et al. 2006). Further, population sizes can also be strongly influenced by interspecific competition, predation, hunting or disturbances (e.g., tourism).

Many of the large herbivore species, native to Western Europe, have shown dramatic decreases in population sizes during the 19th century. However, rather than intra- or interspecific competition, predation or climatic effects, human activities (hunting, habitat fragmentation) were responsible for those reductions, in some cases even local extinctions. In Switzerland, for example, only roe deer (*Caperolus capreolus* L.) and chamois (*Rupicapra rupicapra* L.) showed viable populations at the beginning of the 19th century, while red deer (*Cervus elaphus* L.) and Alpine ibex (*Capra ibex ibex* L.) had disappeared completely. Thereafter hunting pressure decreased and some species slowly started re-immigrating into the country (e.g., red deer), while others had to be reintroduced. Among the latter was the Alpine ibex who was first released in the area of the Swiss National Park (SNP) in 1920 (Schneider 2006). The project was very successful and the number of animals steadily increased to about 15’700 animals (count 2007), separated into several different populations (BAFU 2008a). However, at the beginning of this century quite a few of those populations decreased considerably (Saether et al. 2007), yet the reasons for these decreases are rather unclear.

Several authors suggested that climatic factors could be responsible. For example, Saether et al. (2003) postulated that the winter climate could have a large influence and may be the main bottleneck for population growth of Alpine ibex. Their suggestions are in agreement with the studies conducted by Jacobson et al. (2004) and Grøtan et al. (2008), who found that population fluctuations of ibex were negatively correlated with average winter snow depth. Also, Gressmann et al. (2000) suggested that the topography of the winter habitat was an important factor for limiting the growth rate of ibex populations. Besides trying to link ibex population fluctuations to climatic factors, several research groups within Switzerland are currently investigating whether genetic (inbreeding effects), medical (diseases, physiological problems in winter), or behavioural (reproduction behaviour) parameters as well as hunting could be responsible for the changes (BAFU 2008b). Yet, I am not aware of any results that have been published from these studies to date.

Even though also resource availability could have a strong impact on the population size of ibex (Parker et al. 2009), this factor has, to my knowledge, been completely neglected in the discussion on why Alpine ibex populations decrease in Switzerland. Yet, as for example McKinney et al. (2006) showed, the nutritional status of forage was one reason for changes in bighorn sheep (*Ovis canadensis* Shaw) population sizes. Similarly, Aguirre et al. (1999) reported that winter starvation was one of the major death causes of roe deer in Sweden. Even though winter forage limitation is an important mortality factor for temperate and arctic wild ungulates, also the availability of forage during summer is of importance for survival (Ratcliffe and Mayle 1992, Bassano and Mussa 1998, Brown and Mallory 2007). In particular, females need high nutritious forage to ensure survival of their calves (Brown and Mallory 2007). Indeed, several studies have shown a strong relationship between reproduction success and the female's nutrition status (Verme 1969, Wegge 1975, Verme 1977, White and Bartmann 1983).

Moreover, to understand whether an animal population is constrained by limited resources, it is not only important to gain information on the seasonal differences in forage availability, but also to assess how the composition of the diet varies over the course of a year. Former studies on ibex have shown that a considerable part of their forage is comprised of monocotyledons, the rest by herbs and dwarf-shrubs, conifer needles, mosses and lichens (Schnitter 1962, Frei 1972, ten Houte de Lange 1978, Klansek et al. 1995). Yet, most of these studies did not provide any quantitative data and I am only aware of one study that has assessed how the diet varies over the course of a year (Klansek et al. 1995).

Consequently, the aim of this study was to collect quantitative data on forage composition of Alpine ibex over the course of an entire year using micro-histological analyses of plant fragments in faecal pellets. The study was conducted in the SNP, where human disturbance is kept to a minimum and where the animals are able to forage without disturbance.

Material and Methods

Study area

The SNP is located in the southeastern corner of Switzerland (46°40´N, 10°10´E) and was founded in 1914. Elevation ranges between 1400 and 3174 m above sea level (a.s.l.) and the park occupies an area of approximately 172 km^2. Thereof 50 km^2 are covered by forest (mainly pine forest), 33 km^2 by alpine and 3 km^2 by subalpine grasslands; the other half of the park is dominated by snow, ice, scree and rock (Zoller 1995). The mean annual precipitation was 868.7 ± 155.9 mm and the mean annual temperature 0.57 ± 0.59 °C (mean ± StDev) between 1959 and 2007 (measured at the meteorological station Buffalora, 1970 m a.s.l.). The growing season lasts from early June to the end of September.

One of the major valleys of the SNP - Val Trupchun - is located in the southern most part of the park forming the border to Italy. Its main orientation is north-west to south-east including slopes of highly variable expositions. There are two side valleys in the northern part of Val Trupchun: a bigger one, Val Müschauns and a smaller one, Val Mela. Alpine ibex inhabit the entire area, but remain mostly on south-facing slopes. Their winter habitats are located right above the timberline (blue circles in Figure 1), while they live in a much wider range on high-elevation grasslands and in rocky areas during summer (red circles in Figure 1). I chose Val Trupchun (elevation between 1600 and 3000 m a.s.l.) and Val Müschauns (elevation between 1900 and 2900 m a.s.l.) as my study area. In both valleys the timberline reaches up to 2200 m a.s.l.. There is no hunting in the SNP and human activities are restricted to hiking on trails.

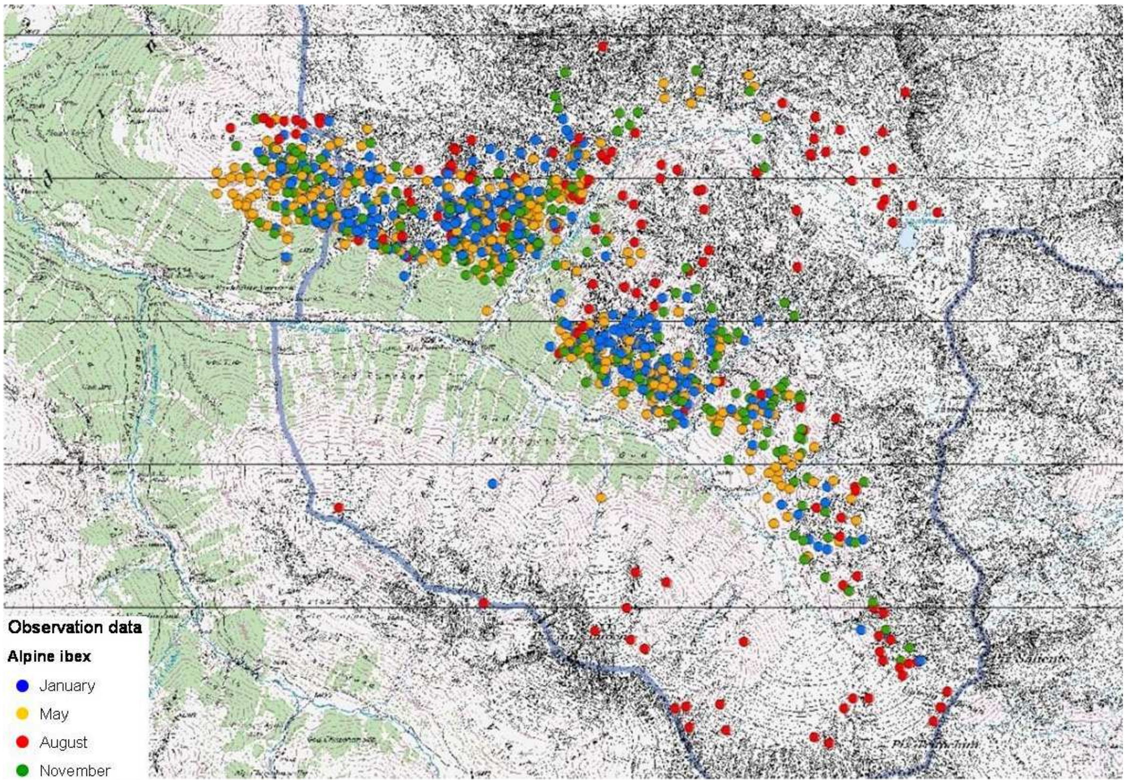


Figure 1: Observation of Alpine ibex in Val Trupchun and Val Müschauns (SNP) at different times of the year from 1997 to 2005 (Haller 2006).

Pellet sampling

I collected fresh faecal pellets of the Alpine ibex in both Val Trupchun and Val Müschauns at different locations in four different seasons throughout 2008: 1) in the winter habitat in mid-February, 2) in the migration area between winter and summer habitat in mid-May, 3) in the summer habitat in mid-August and 4) in the migration area between summer and winter habitat in mid-November. Each time I randomly collected 20 samples (1 sample = 1 pellet group) by walking transects starting at the valley bottom and moving uphill (= total of 80 samples in four seasons). The distance between transects was ten meters and I walked as many transect as necessary to obtain the 20 samples. The minimal distance between two samples included into the collection was as well ten meters. The samples were stored in the freezer until further processed in the laboratory.

Laboratory analyses

For preparation and analysis of the faecal samples I autoclaved 5 g of each frozen sample. The sample was then crushed and ground in a mortar. From this homogenized mixture I put 2.5 g into a lab blender and covered it with water. The blended sample was rinsed through a 0.1 mm sieve, washed with water and then with 70% alcohol. After washing, the sample was transferred into 70% alcohol to preserve it (de Jong et al. 1995).

For conducting the micro-histological analysis the entire sample was placed into a petri dish and allowed to settle for 15 minutes. I took ten random grab samples consisting of one to two drops with a Pasteur pipette, put each of them on a microscope slide and covered them. The slides were then viewed with a microscope with a 250 x magnification. On each slide I selected ten epidermis fragments with a minimum size of 0.02 mm^2 along transects starting at the left and the top of the slide, respectively, and assigned the fragments to a plant species, a genera or a group of several plant species (see Table 1). Whenever possible I identified the selected plant fragments to the species or genus level. However, due to the high similarity between some plant fragments this was not always possible. In these cases I assigned the fragments to artificial (very similar grass species) or functional (forbs, dwarf-shrubs, mosses, ferns) groups (Table 1). Altogether I analysed 100 fragments (10 grab samples x 10 fragments) per sample (Katona and Altbacker 2002), thus a total of 8000 fragments (100 fragments x 80 samples) were identified.

Reference database

Identification of the species or species groups was achieved by comparing the fragments with reference slides available in a database (http://wwwtest.wsl.ch/kotanalyse/kotanalyse/anmelden.html) containing slides of plant epidermis collected within the study area. Existing deficits in the database were completed as follows: Plants (leaves or needles) were sampled in the study area, cut into pieces (about 0.5

cm^2) and inserted in sodium hypochlorite 2.5% (javel water). After several hours or days the epidermis could be peeled away and was placed on a microscope slide. The fragment was covered with a small layer of glycerine and the cover glass fixed with nail polish.

Table 1: Plant species, genera and species groups identified in faecal pellets of Alpine ibex. Names in parenthesis indicate species with similar epidermis characteristics, which were difficult to identify.

Monocotyledons:	
Cyperaceae	*Carex sp.*
	Elyna myosuroides (Vill.) Fritsch
	unidentified *Cyperaceae*
Poaceae:	*Festuca ovina* L.
	Festuca rubra L./*Festuca violacea* Gaudin
	Nardus stricta L.
	Sesleria caerulea (L.) Ard.
	group 1: Agrostis capillaris L., *Anthoxanthum odoratum* L., *Dactylis glomerata* L., *Trisetum flavescens* (L.) P. Beauv., *(Briza media* L.)
	group 2: Deschampsia cespitosa (L.) P. Beauv., *Deschampsia flexuosa* (L.) Trin., *Phleum alpinum* L., *(Helictotrichon pubescens* (Huds.) Pilg., *Briza media)*
	group 3: Poa pratensis L., *(Helictotrichon pubescens)*
	unidentified *Poaceae*
Dicotyledons:	
Herbs:	Herbs
Dwarf-shrubs:	*Erica carnea* L.
	Rhododendron sp.
	Vaccinium vitis-ideae L.
	unidentified Dwarf-shrubs
	unidentified Dicotyledons
Conifers:	*Juniperus communis* L.
	Larix decidua Mill.
	Picea abies (L.) H. Karst.
	Pinus sp.
	unidentified Conifers
Others:	Ferns
	Mosses
	unidentified fragments

Statistical analyses

For the statistical analyses I selected all the species and groups of plant species with a frequency of occurrence of at least 5% in one season (expect the group “Others”, which was included since these species would otherwise not be covered). The data were log-transformed [log (x+1)] to fulfil the homogeneity and normality criteria. To assess the differences in diet composition I conducted ANOVA’s for all the species and species groups listed in Table 1 (independent variables) over the course of the year (dependent variables). In addition I performed ANOVA’s followed by Tukey-HSD post-hoc tests using the independent variables “*Cyperaceae*”, “*Poaceae*”, “Total Monocotyledons”, “Herbs”, “Dwarf-shrubs”, “unidentified Dicotyledons”, “Total Dicotyledons”, “Total Conifers” and “Total Others” and the dependent variable season. I also conducted a detrended correspondence analysis (DCA) using Canoco for Windows 4.5 to investigate differences between the seasons and to find the main factors (plant species, genera or plant species groups) describing them. To assess differences between seasons, axes scores (from axis 1 and axis 2) were tested with a one-way ANOVA followed by a Tukey-HSD post-hoc test for multiple comparisons for the seasons (SPSS for Windows 15.0).

Results

The 8000 epidermal fragments determined from the 80 faecal samples were assigned to one of 25 plant species, genera or plant species groups shown in Table 1. However, for the statistical analyses I only used the 14 plant species, genera or plant species groups with frequency of occurrence > 5% in at least one of the four seasons. On average Alpine ibex consumed 69.5% (seasonal variation from 64.8 - 73.4%) monocotyledons (graminoids), 24.3% (17.6 - 33.9%) dicotyledons (herbs, dwarf-shrubs), 4.9% (0.1 - 7.8%) conifers and 1.4% (1.2 - 1.8%) other plant species (ferns, mosses, unidentified fragments; Table 2). Monocotyledons were the dominant forage at all times of the year and did not significantly differ between the seasons (Table 2, 3, Figure 2). However, when separating the consumption of monocotyledons into *Cyperaceae* and *Poaceae,* significantly different seasonal frequencies were detected (Table 3). For example, total *Cyperaceae* and *Carex sp*. were consumed significantly more often in winter and spring, compared to summer and autumn, while the consumption of *Elyna myosuroides* was highest in spring, but did not differ among the other three seasons. Total *Poaceae* consumption was significantly higher in both summer and autumn compared to spring, but did not differ from the winter values. *Festuca ovina* was significantly more often eaten in autumn and winter than summer and *F. rubra/F. violacea* were more often found in autumn samples compared to those sampled in spring and winter (Table 3). *Poaceae* within group 1 were significantly more often identified in the dung collected in summer and autumn, while *Poaceae* within group 2 had a significant peak in summer. Group 3 *Poaceae* were significantly more often consumed in summer than in spring. No significant seasonal differences were found in the consumption of *Sesleria caerulea* and also the amount of *Poaceae* that I could not identify was not different over the course of the year (Table 2, 3, Figure 2). Of all monocotyledons, *F. rubra/F. violacea* and *Sesleria caerulea* were consumed most frequently throughout the year and had frequencies of over 7% regardless of the season (Table 2).

Herb consumption was highest in summer (22.2%), lowest in winter (1.5%) and significantly differed between all the seasons except spring and autumn (Table 2, 3, Figure 2). Thus, herb consumption mirrored the annual growth and development of herbaceous forage. Dwarf-shrubs did not differ significantly over the course of the year (Table 3, Figure 2). Coniferous plants had a significantly lower consumption rate in summer (0.1%) compared to the other seasons with *Larix decidua* being the most frequently consumed species (Table 2, 3). Mosses and ferns were eaten only scarcely: mosses were found in similar frequencies during all seasons. Ferns were only found in winter and autumn, but the amount was so small that there was no difference to spring and summer, when no ferns were consumed.

Table 2: Number of fragments (No.) and frequency of occurrence (%) of plant species, genera or plant species groups identified in the 20 faecal samples of Alpine ibex in four different seasons in the SNP. The grand total results from the highlighted totals.

	Winter		Spring		Summer		Autumn		*p*-value
	No.	%	No.	%	No.	%	No.	%	
Monocotyledons:									
Cyperaceae:									
Carex sp.	249	12.45	247	12.35	36	1.80	86	4.30	<0.001
Elyna myosuroides	56	2.80	143	7.15	35	1.75	69	3.45	<0.001
unidentified *Cyperaceae*	51	2.55	30	1.50	19	0.95	30	1.50	0.057
Total *Cyperaceae*	356	17.80	420	21.00	90	4.50	185	9.25	<0.001
Poaceae:									
Festuca ovina	141	7.05	108	5.40	79	3.95	194	9.70	0.001
Festuca rubra/F. violacea	155	7.75	141	7.05	169	8.45	204	10.20	0.025
Nardus stricta	3	0.15	7	0.35	0	0.00	0	0.00	0.020
Sesleria caerulea	225	11.25	176	8.80	173	8.65	187	9.35	0.341
group 1*	58	2.90	27	1.35	131	6.55	158	7.90	<0.001
group 2**	117	5.85	86	4.30	283	14.15	149	7.45	<0.001
group 3***	103	5.15	74	3.70	121	6.05	95	4.75	0.018
unidentified *Poaceae*	310	15.50	296	14.80	249	12.45	288	14.40	0.606
Total *Poaceae*	1112	55.60	915	45.75	1205	60.25	1275	63.75	0.001
Total Monocotyledons	1468	73.40	1335	66.75	1295	64.75	1460	73.00	0.187
Dicotyledons:									
Herbs:	30	1.50	174	8.70	444	22.20	114	5.70	<0.001
Dwarf-shrubs:									
Erica carnea	3	0.15	40	2.00	0	0.00	25	1.25	<0.001
Rhododendron sp.	19	0.95	3	0.15	5	0.25	15	0.75	0.160
Vaccinium vitis-ideae	5	0.25	2	0.10	5	0.25	7	0.35	0.591
unidentified Dwarf-shrubs	133	6.65	97	4.85	98	4.90	169	8.45	0.053
Total Dwarf-shrubs	160	8.00	142	7.10	108	5.40	216	10.80	0.078
unidentified Dicotyledons	162	8.10	170	8.50	126	6.30	100	5.00	0.029
Total Dicotyledons	352	17.60	486	24.30	678	33.90	430	21.50	0.002

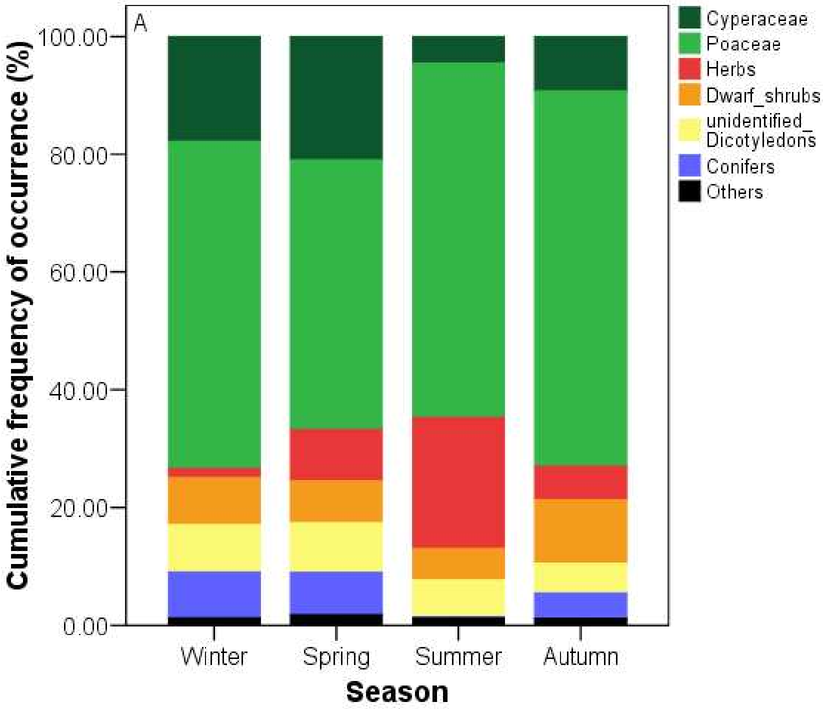
Table 2: continued

	Winter		Spring		Summer		Autumn		*p*-value
	No.	%	No.	%	No.		No.	%	
Conifers:									
Juniperus communis	0	0.00	1	0.05	0	0.00	1	0.05	0.575
Larix decidua	59	2.95	89	4.45	1	0.05	42	2.10	<0.001
Picea abies	3	0.15	6	0.30	0	0.00	0	0.00	0.193
Pinus sp.	52	2.60	22	1.10	1	0.05	42	2.10	0.011
unidentified Conifers	41	2.05	25	1.25	0	0.00	1	0.05	<0.001
Total Conifers	155	7.75	143	7.15	2	0.10	86	4.30	<0.001
Others:									
Ferns	6	0.30	0	0.00	0	0.00	1	0.05	0.261
Mosses	8	0.40	8	0.40	18	0.90	5	0.25	0.329
unidentified fragments	11	0.55	28	1.40	7	0.35	18	0.90	0.047
Total Others	25	1.25	36	1.80	25	1.25	24	1.20	0.680
TOTAL	2000	100.00	2000	100.00	2000	100.00	2000	100.00	

*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)*



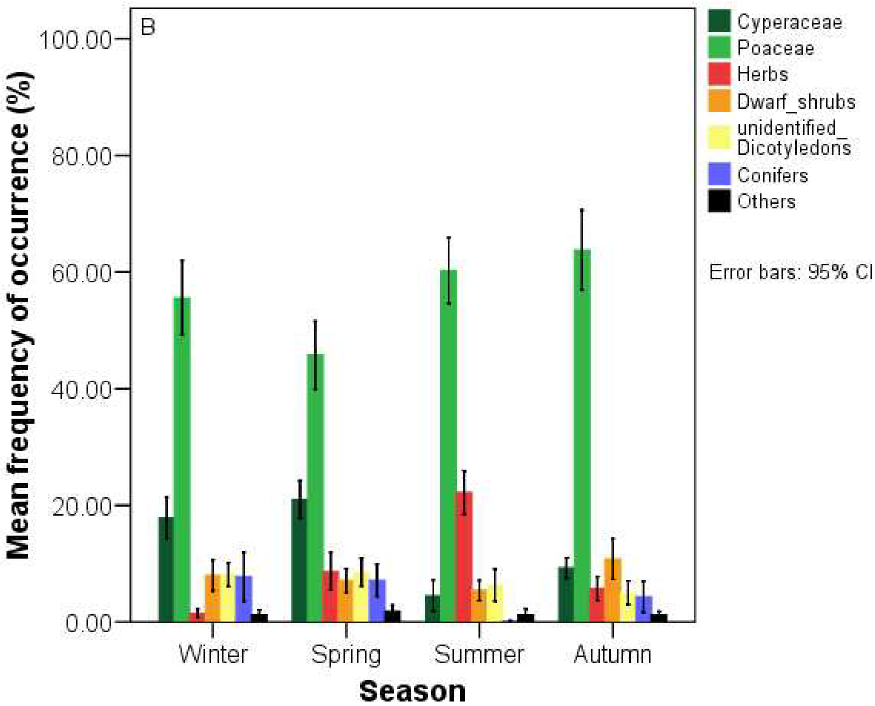


Figure 2: A: Cumulative frequency of occurrence (%) and of the main plant groups in the four seasons. **B:** Mean frequency of occurrence (%) of the main plant groups in the four seasons. n = 20 for each season.

Table 3: Multiple comparisons of the main plant groups between the seasons (Tukey-HSD). Different letters indicate significantly different values. The significance level is at alpha = 0.05 and n = 20 for each season.

	Winter	Spring	Summer	Autumn	*p*-value
Monocotyledons:					
Cyperaceae	a	a	c	b	<0.001
Poaceae	ab	b	a	a	0.001
Total Monocotyledons	a	a	a	a	0.187
Dicotyledons:					
Herbs	c	b	a	b	<0.001
Dwarf-shrubs	a	a	a	a	0.078
unidentified Dicotyledons	a	a	ab	b	0.029
Total Dicotyledons	b	ab	a	b	0.002
Conifers:					
Total Conifers	a	a	c	b	<0.001
Others:					
Total Others	a	a	a	a	0.680

Figure 3 shows the DCA of the diet samples. The first two axes explained 49.9% (axis 1: 33.7% and axis 2: 16.2%) of the variance in the data. Axis 1 was associated with time of the year and explained how the forage composition differed between the four seasons ($F_{3,76}$ = 75.7, p < 0.001; Figure 3, 4), while axis 2 did not explain any of the temporal variation ($F_{3,76}$ = 1.6, p = 0.203; Figure 3, 4), but rather differences between the individual ibex. Winter and spring were characterized by the relatively high consumption of conifers, *Cyperaceae*, and *Sesleria caerulea* (Figure 5, see also Table 2). The samples collected during summer were separated from the other samples by the high amount of herbs and *Poaceae* species within group 1 and group 2 as well as the low amount of conifers and *Cyperaceae*. The autumn samples contained higher amounts of *Festuca ovina, F. rubra/F. violacea* and dwarf-shrubs (Table 2, Figures 3, 5).

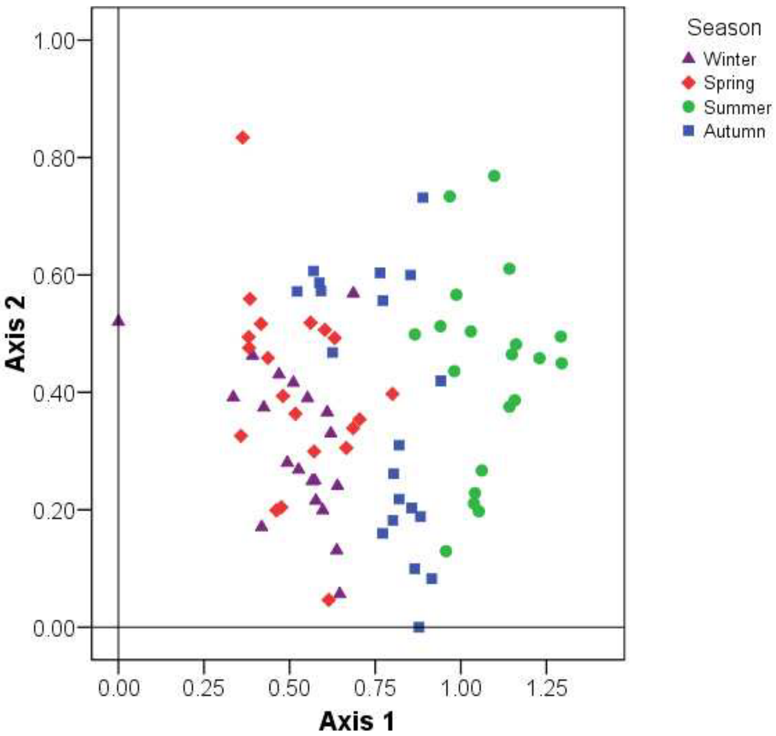


Figure 3: DCA of the forage samples of Alpine ibex collected throughout the four seasons. n = 20 for each season.

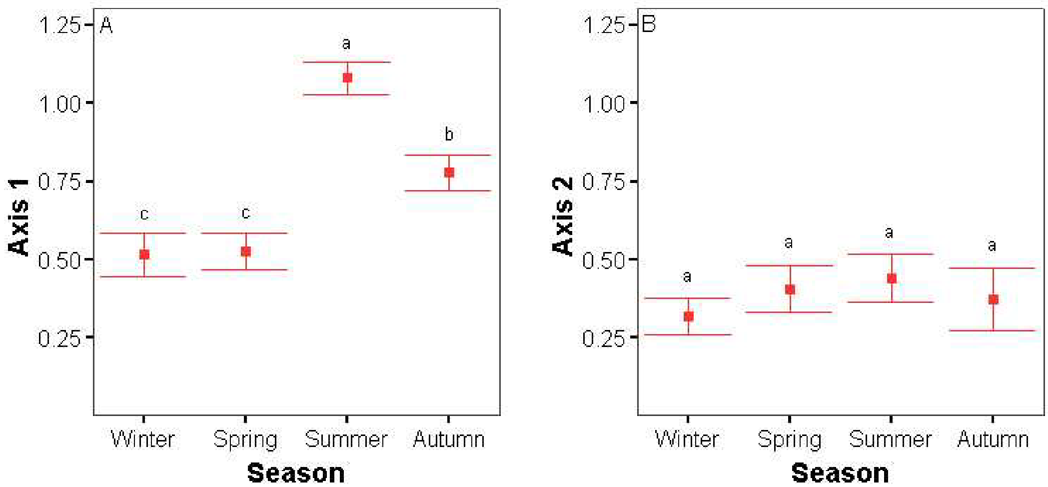


Figure 4: Mean axes scores of the DCA for the four seasons: **A**: axis 1; **B**: axis 2. The error bars show the 95% CI of the means. Different letters indicate significantly different mean axes scores. The significance level is at alpha = 0.05 and n = 20 for each season.

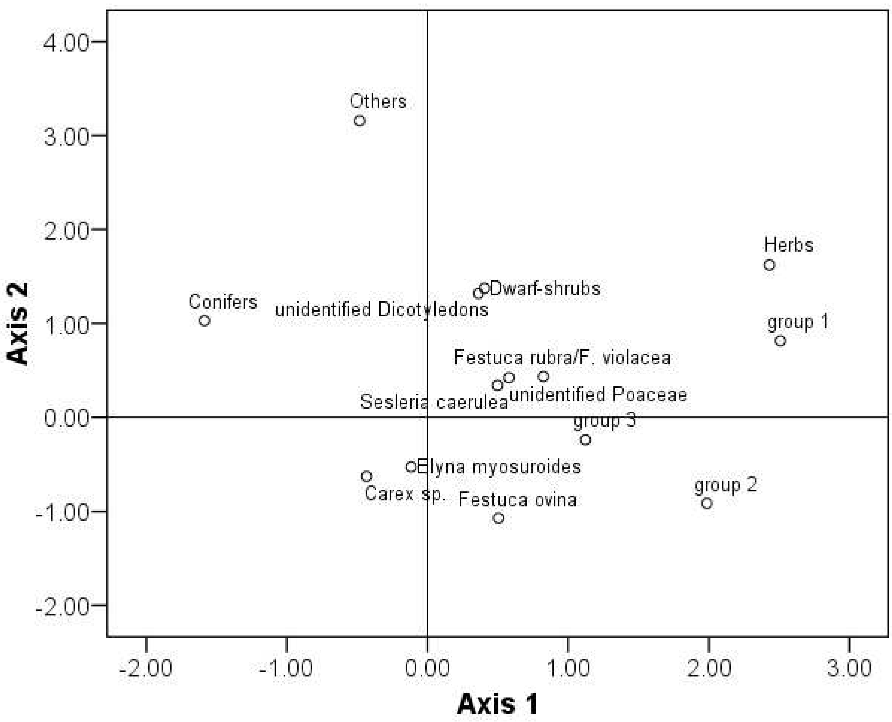


Figure 5: DCA of the 14 plant species, genera or plant species groups contained in the dung samples of Alpine ibex collected throughout the four seasons.

Discussion

This study showed that the diet composition of Alpine ibex significantly differed over the course of the year in the SNP, but was dominated by monocotyledons regardless of the season. This confirms that Alpine ibex are primarily grazers or grass roughage eaters (Hofmann 1989) similar to other species within the genus *Capra*: for example in the rumen of Spanish ibex (*Capra pyrenaica* Schinz) between 78.2 - 83.8% of all the plants were graminoids (Martinez 2001). Also Sibirian ibex (*Capra ibex sibirica* Pallas), Dagestan tur (*Capra cylindricornis* Blyth) and Kuban ibex (*Capra ibex caucasica* Güldenstaedt and Pallas) consumed between 80 - 95% graminoids (Heptner et al. 1966, Schaller 1977). Herbs contributed considerably to the ibex diet during summer, when they were grazing on high-elevation grasslands and in rocky areas. The larger amount of conifers in winter and spring can be explained by the fact that the animals stay in or close to the forest during these seasons.

The Alpine ibex is a highly dimorphic species (Nievergelt and Zingg 1986). Due to the larger body size males have lower energy requirements per unit mass, which means they are able to digest forage with higher fiber and lower protein content (low quality diet) more efficiently than the smaller females (Geist 1974, Villaret et al. 1997, Ruckstuhl and Neuhaus 2000, Perez-Barberia et al. 2007). Indeed it has been shown that female Nubian ibex (*Capra ibex nubiana* Cuvier) were more selective, choosing higher quality forage and spending more time foraging than males (Gross et al. 1995). Unfortunately, it was impossible to distinguish between pellets of males and females in the field. For this reason, I did not include this aspect in my study and decided to collect the samples randomly. The fact that there were no true groups in the DCA's indicates that there likely is no large difference in the diet composition of male and female ibex in my study area.

I could not detect another study that has used faecal analysis to determine the diet composition of ibex. However, my findings were in range with those of other authors who investigated the diet compositions of *Capra ibex* by rumen analyses or direct observations. They all showed that monocotyledons were the most important forage regardless of the season, but the percentages reported differ widely: Klansek et al. (1995) reported the amount of graminoids in rumen to range between 84.6 - 94% in a study conducted in different colonies in Switzerland, while Schnitter (1962), Frei (1972) and ten Houte de Lange (1978) observed ranges of 39 to 76% by direct observation of the animals. I could not find another study that separated monocotyledons into *Cyperaceae* and *Poaceae* as I did and therefore I cannot compare those results with the literature. However, Couturier (1962), who observed ibex in the Swiss, French and Italian Alps, especially in the Gran Paradiso National Park, mentioned the genus *Festuca* as an important winter and spring forage, but did not provide any quantitative data. My results showed, in contrast, a significant higher consumption of *Festuca* species in autumn compared to spring and summer. Furthermore, different authors noted that graminoid species *Anthoxanthum odoratum alpinum, Carex sempervirens, C. curvula, Festuca rubra, F. violacea, F. pumila, Dactylis glomerata, Poa alpine* and *Sesleria caerulea* as important plant species eaten by ibex (Schnitter 1962, Frei 1972, ten Houte de Lange 1978). With the exception of *Festuca pumila* these species all grew in the SNP and were consumed.

Dicotyledons were the second most frequently consumed group of plants in my study. Again, the studies using direct observations showed higher (up to 38%; Schnitter 1962; Frei 1972; ten Houte de Lange 1978), the one using rumen analyses lower averages (7.5%; Klansek et al.1995) compared to my study. While the average amount of conifers in the data presented by ten Houte de Lange (1978) and Klansek et al. (1995) did not differ much (2% and 2.4% respectively), ten Houte de Lange (1978) reported a large difference in consumption frequencies between the seasons (0 - 7%) at Piz Albris in the Swiss Alps. In contrast, Klansek et al. (1995) found no seasonal variability in the amount of coniferous plants consumed. Overall, the average proportions of coniferous plants consumed in these studies were considerably lower than the 4.9% I found. In contrast to results reported from Gran Paradiso National Park, where ibex consumed mosses and lichens throughout the entire year with highest values in winter (Couturier 1962), mosses contributed only a small amount to the diet in my study and consumption did not differ between the seasons. One possibility is that Alpine ibex were not forced to feed on low quality mosses, since they found enough higher quality forage.

The high variability in the amount of specific plants consumed by ibex reported in the literature can have various origins. The availability of plants can vary over the year and between different habitats. Additionally plants alter in their nutrient or vitamin content, their flavour or their shape and therefore show different digestibilities. Thus, depending on the different digestibility of plants it is possible that certain species are over-, others underestimated when conducting forage composition analyses. Some studies compare rumen analyses or oesophageal fistula valve with faecal analyses and state that in faecal analyses graminoids might be overestimated compared to the better digestible forbs (Bartolome et al. 1995, Bartolome et al. 1998). However, other authors found no significant differences between these methods (Anthony and Smith 1974, Homolka and Heroldova 1992, Mohammad et al. 1995, Chapuis et al. 2001, Henley et al. 2001). The possible sources of error in micro-histological analysis technique are discussed in Holechek et al. (1982) and Alipayo et al. (1992), yet it seems to be one of the best techniques to analyse the diet composition of large herbivores (Mohammad et al. 1995).

Altogether, with the present data we obtain a relatively detailed insight in the diet composition of Alpine ibex over the course of the year. However, there is further research needed to investigate the availability of the forage resources in the area and to which extend this forage is used by the animals.

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

	Wi1	Wi2	Wi3	Wi4	Wi5	Wi6	Wi7	Wi8	Wi9	Wi10	Wi11	Wi12	Wi13	Wi14	Wi15	Wi16	Wi17	Wi18	Wi19	Wi20	Winter Total
Monocotyledons:																					
Cyperaceae:																					
Carex sp.	15	11	21	19	16	4	13	10	7	5	12	5	16	14	16	3	22	16	12	12	249
Elyna myosiroides	4	0	4	2	3	4	6	3	1	1	4	1	4	2	3	0	3	4	4	3	56
unidentified *Cyperaceae*	4	1	9	0	5	4	2	5	2	1	5	0	4	0	0	0	2	1	4	2	51
Poaceae:																					
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
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
unidentified *Poaceae*	5	15	22	10	10	19	12	14	10	16	21	9	22	9	17	29	24	19	15	12	310
Dicotyledons:																					
Herbs	2	0	1	2	0	1	2	0	2	2	0	3	0	0	0	5	2	4	2	2	30
Dwarf-shrubs																					
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 vitis-ideae	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	2	5
unidentified Dwarf-shrubs	13	4	9	6	2	4	9	2	9	18	1	12	0	11	8	4	0	6	9	6	133
unidentified Dicotyledons	8	1	2	13	3	8	8	11	6	3	13	8	3	7	10	5	14	15	14	10	162
Conifers:																					
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
unidentified conifers	3	4	0	0	7	0	3	1	6	2	2	1	1	2	3	2	2	1	1	0	41
Others:																					
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
unidentified fragments	0	1	0	0	1	0	0	0	1	0	2	0	1	1	0	2	1	0	0	1	11
Total	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	2000

*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 Alpine ibex in spring in the SNP.

	Sp1	Sp2	Sp3	Sp4	Sp5	Sp6	Sp7	Sp8	Sp9	Sp10	Sp11	Sp12	Sp13	Sp14	Sp15	Sp16	Sp17	Sp18	Sp19	Sp20	Spring Total
Monocotyledons:																					
Cyperaceae:																					
Carex sp.	8	21	23	7	12	5	11	3	9	12	7	14	15	17	16	10	15	4	17	21	247
Elyna myosiroides	3	5	1	6	11	3	6	5	11	13	5	9	8	9	8	16	1	11	12	0	143
unidentified *Cyperaceae*	0	0	6	6	4	0	1	0	0	0	3	0	0	0	0	1	0	5	4	0	30
Poaceae:																					
Festuca ovina	5	6	6	3	8	1	5	6	0	10	6	7	4	6	6	7	8	3	2	9	108
Festuca rubra/F. violacea	3	7	5	6	4	4	10	5	3	6	6	11	7	7	3	14	9	9	10	12	141
Nardus stricta	1	2	0	0	0	0	0	0	0	1	0	0	2	0	1	0	0	0	0	0	7
Sesleria caerulea	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
unidentified *Poaceae*	6	20	14	20	7	21	16	20	4	25	18	20	8	17	18	14	11	10	13	14	296
Dicotyledons:																					
Herbs	25	2	4	7	4	8	15	13	24	3	5	5	7	9	13	1	9	15	1	4	174
Dwarf-shrubs																					
Erica carnea	0	1	4	5	3	1	1	0	3	0	4	2	4	2	1	0	2	5	1	1	40
Rhododendron sp.	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	3
Vaccinium vitis-ideae	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
unidentified Dwarf-shrubs	4	4	9	2	11	9	0	4	11	2	1	7	8	6	5	0	4	5	0	5	97
unidentified Dicotyledons	15	4	2	7	11	19	6	11	12	3	6	10	7	10	10	4	19	10	2	2	170
Conifers:																					
Juniperus communis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Larix decidua	25	4	2	1	2	11	8	10	6	0	11	1	0	0	0	3	0	2	2	1	89
Picea abies	0	2	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	6
Pinus sp.	0	0	8	5	3	0	0	0	0	0	1	0	0	0	0	0	0	0	5	0	22
unidentified conifers	0	2	1	0	0	4	0	0	3	3	0	1	6	2	0	0	0	0	0	3	25
Others:																					
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
unidentified fragments	0	2	0	0	1	0	0	1	3	1	0	3	2	1	1	0	4	0	1	8	28
Total	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	2000

*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 Alpine ibex in summer in the SNP.

	Su1	Su2	Su3	Su4	Su5	Su6	Su7	Su8	Su9	Su10	Su11	Su12	Su13	Su14	Su15	Su16	Su17	Su18	Su19	Su20	Summer Total
Monocotyledons:																					
Cyperaceae:																					
Carex sp.	1	0	0	3	1	2	3	2	4	3	1	4	2	0	4	2	0	2	2	0	36
Elyna myosiroides	2	1	0	2	3	4	0	1	13	2	1	2	0	0	3	0	0	0	1	0	35
unidentified *Cyperaceae*	1	1	0	1	1	2	0	0	9	0	0	1	0	0	2	1	0	0	0	0	19
Poaceae:																					
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
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
unidentified *Poaceae*	12	8	11	18	10	10	16	17	10	14	21	8	15	13	7	11	12	15	10	11	249
Dicotyledons:																					
Herbs	37	32	36	22	17	12	25	14	11	25	11	12	19	29	30	20	24	18	26	24	444
Dwarf-shrubs																					
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 vitis-ideae	2	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	5
unidentified Dwarf-shrubs	5	9	6	2	3	2	4	2	2	6	4	5	5	4	16	7	4	3	5	4	98
unidentified Dicotyledons	4	1	3	1	23	2	2	2	0	0	2	8	5	12	10	10	9	8	14	10	126
Conifers:																					
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
unidentified conifers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Others:																					
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
unidentified fragments	2	2	0	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	7
Total	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	2000

*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 Alpine ibex in autumn in the SNP.

	Au1	Au2	Au3	Au4	Au5	Au6	Au7	Au8	Au9	Au10	Au11	Au12	Au13	Au14	Au15	Au16	Au17	Au18	Au19	Au20	Autumn Total
Monocotyledons:																					
Cyperaceae:																					
Carex sp.	3	1	10	2	1	1	5	1	4	9	5	9	4	7	2	4	5	3	4	6	86
Elyna myosiroides	1	1	0	3	10	5	2	2	5	2	2	2	7	2	6	6	3	3	5	2	69
unidentified *Cyperaceae*	0	0	3	0	0	1	1	0	1	5	6	0	1	1	4	3	0	1	2	1	30
Poaceae:																					
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
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
unidentified *Poaceae*	10	21	7	12	19	22	10	3	17	6	6	15	22	12	12	22	19	10	21	22	288
Dicotyledons:																					
Herbs	12	7	4	4	2	4	7	12	6	4	3	2	6	17	4	1	3	13	2	1	114
Dwarf-shrubs																					
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 vitis-ideae	0	0	2	1	0	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	7
unidentified Dwarf-shrubs	4	13	8	11	10	6	9	25	4	4	5	5	6	16	3	3	7	18	7	5	169
unidentified Dicotyledons	10	1	7	3	6	4	8	16	5	0	3	2	1	13	1	0	6	8	5	1	100
Conifers:																					
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
unidentified conifers	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Others:																					
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
unidentified fragments	2	2	1	1	2	3	1	2	0	0	0	0	0	2	0	0	2	0	0	0	18
Total	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	2000

*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)*