Diet of the Alpine mountain hare (*Lepus timidus varronis* MILLER 1901) in a subalpine ecosystem

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Abstract

The diet of the Alpine mountain hare (*Lepus timidus varronis*) was studied throughout microhistological analysis of faecal pellets in the Swiss National Park (eastern Swiss Alps). Samples were collected seasonally in 33 different sampling sites. For each season, 11 samples collected in a subalpine area were analysed. From each sample two faecal pellets were randomly selected, milled and 200 plant epidermal fragments were identified with an identification key created throughout a collection of reference slides.

On average the 44 samples analysed were composed of 47.00% gymnosperm and 32.47% monocotyledons. However, Alpine mountain hare also consumed in small percentage dycotyledons like dwarf shrubs, mainly ericaceous shrubs, and forbs.

Winter samples were significantly different from samples from the other seasons by a high amount (71.91%) of gymnosperms. Variations between the other seasons were relatively small.

This study tends to confirm the opportunistic feeding strategy of this species by the high amount of gymnosperm identified even in summer samples. Nevertheless, our results also showed a tendency in a selection of high energy food items like forbs and reproductive plant part when available. High consumption of gymnosperm throughout the year displays the avoidance of open pasture observed in radio-tracking studies on Alpine mountain hare.

Keywords Alpine mountain hare, *Lepus timidus varronis*, diet selection, microhistological analysis, gymnosperms, Swiss National Park

Résumé

Le régime alimentaire du lièvre variable (*Lepus timidus varronis*) a été étudié dans le Parc National Suisse (Alpes suisses orientales) en utilisant la méthode des analyses microhistologiques des fèces. Les échantillons ont été récoltés saisonnièrement dans 33 différents points d'échantillonnage. Pour chaque saison 11 échantillons ont été analysés. Les échantillons analysés proviennent de la partie subalpine de la zone d'étude. Pour chaque échantillon 200 fragments ont été identifiés à partir de 2 crottes sélectionnées aléatoirement. Les identifications ont été effectuées grâce à une clé de détermination crée à partir d'une collection de lames de référence.

En moyenne, les 44 échantillons analysés étaient composés de 47.00% de gymnospermes et de 32.47% de monocotylédones. Cependant, le lièvre variable des Alpes consomme aussi des dicotylédones comme des arbustes nains, principalement des éricacées, et des plantes herbacées.

Les échantillons hivernaux se différencient significativement des autres par un taux élevé de gymnospermes (71.91%). Les variations entre les autres saisons sont moindres.

Cette étude tend à confirmer une stratégie de nutrition opportuniste déjà observée pour cette espèce. Néanmoins, nos résultats montrent aussi une tendance à sélectionner de la nourriture avec des valeurs nutritionnelles élevées comme les plantes herbacées et les parties reproductives des plantes si elles sont disponibles. Une consommation élevée de gymnospermes tout au long de l'année confirme la tendance à éviter les prairies ouvertes. Ce qui a été observée pendant des suivi radio-télémétriques effectuées lors d'études précédents.

Mots-clés Lièvre variable des Alpes, *Lepus timidus varronis*, régime alimentaire, analyses microhistologiques, gymnospermes, Parc National Suisse

Introduction

The mountain hare (*Lepus timidus*) is a Lagomorph species with a Palaearctic distribution (Angerbjorn and Flux 1995; Mitchell-Jones et al. 1999). Throughout the last ice age this species was widespread south of the ice-rim. After the end of this ice age the distribution of mountain hare was reduced gradually (Thulin 2003). This species can be subdivided in 16 subspecies of wich 6 are present in Europe. It is a species very well adapted to its environment, capable to survive under harsh conditions and with limited food sources (Angerbjorn and Flux 1995).

The Alpine mountain hare (*Lepus timidus varronis*) is one of the 6 European subspecies and it is endemic of the Alps where it forms a relict population. It is distributed throughout the Alpine chain between 1500 and 3500 m (Angerbjorn and Flux 1995; Salvioni 1995; Mitchell-Jones et al. 1999; Thulin and Flux 2003), at lower altitudes it is replaced by the brown hare (*Lepus europaeus*) (Salvioni 1995; Slotta-Bachmayr 1999). In a small altitude range the two species can be found sympatrically (Meile 1984).

IUCN conservation status of the Alpine mountain hare is *Least Concern* (Smith and Johnston 2008). However, in some Alpine areas population of this species seems to decline gradually (Mitchell-Jones et al. 1999; Nodari 2006). Additionally, Alpine mountain hare might suffer from the consequences of global climate change with the reduction of its potential habitat and the spreading of brown hare distribution (Hackländer et al. 2008).

Knowledge of the feeding ecology of a species allows a better understanding of the interactions between a species and its environment. Food requirements of an animal are principally determined by the type of its digestive system and the body size (Caughley and Sinclair 1994). Furthermore, in order to assess the potential responses of Alpine mountain hare to climate change it is fundamental to determine its ecological requirements such as food demands (Rao et al. 2003*a;* Paupério and Alves 2008). Mountain hare are year-round active herbivores mainly active at night (Angerbjorn and Flux 1995) and therefore has to survive under extreme variation in climatic conditions and in resource availability. Consequently it is important not only to determine mountain hare trophic exigencies but also to assess seasonal variation in its diet.

The diet selection of mountain hare has been largely studied in Scandinavia (Pehrson 1979; Pulliainen and Tunkkari 1987; Johannessen and Samset 1994), in Scotland (Hulbert et al. 2001; Rao et al. 2003*a*) and in Ireland (Wolfe et al. 1996; Dingerkus and Montgomery 2001; Strevens and Rochford 2004). However Alpine mountain hare is less studied (Barbieri 1998; Slotta-Bachmayr 1999; Nodari 2006). The dietary requirements of Alpine mountain hare have been analyzed in a study in the Austrian Alps (Loidl 1997) and in one study about this species ecology in the French Alps (Bouche 1989).

The aims of this work are to describe the diet of a population of Alpine mountain hare in a subalpine ecosystem and to assess its seasonal variations. Diet selection is investigated through microhistological analysis of faecal pellets, a method based on anatomical characteristics of plant epidermal cells. Epidermal cells are very strong and support herbivore digestive process (Chapuis 1980). Faecal pellets are found 90% on feeding places, this providing good indication of selected feeding places (Bouche 1989; Hewson 1989).

Material and methods

Study area

This study was carried out in the Swiss National Park, a restricted nature reserve (IUCN category 1) located in the south-eastern Swiss Alps (46°42'N, 10°06'). The Park has an area of 170.3 km^2 and the elevation ranges from 1380 to 3173 m above sea level. Coniferous forest covers 29.36% of the surface of the Park, alpine grassland 19.38% and subalpine grassland 1.76%. The remainder 49.50% comprises rocks, snow and ice. The most abundant coniferous species are mountain pine (*Pinus mugo* subs. *uncinata*) Swiss mountain pine (*Pinus mugo* subs. *mugo*), Swiss stone pine (*Pinus cembra*). Swiss mountain pine represents almost 30% of the total coniferous forest. European larch (*Larix decidua*); Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) are less frequent (Haller 2006). Throughout a Geographical Information System (GIS) analysis of the Swiss National Park data from HABITALP – Project (Lotz 2006), there resulted 12 primary habitat types in the area of the Park (Rehnus 2009).
The climate is continental (Haller 2006), average annual temperature and precipitation are 0.2 °C ± 0.76 and 925 mm ± 162, respectively (means ± standard deviation; recorded in the study area). The growing season begins early June and ends late September.

Faecal pellet collection

Faecal pellets were sampled between July 2007 and May 2008. In order to analyze the seasonal variation in the diet, faeces were sampled in summer (July and August), autumn (October), winter (February) and spring (May). Faeces were samples in 33 trial plots of 20x20 m at altitudes comprised between 1658 and 2578 m above sea level. Plots are distributed in 11 of the 12 characteristic habitats presents in the Swiss National Park; rock was excluded as not suitable habitat for hares. Samplings were done in 2 phases. The first phases, called "cleaning phases"

consisted in cleaning the plots from all Alpine mountain hare faecal pellets. The second phase, the "controlling phase" consisted in cleaning the plots three nights after the cleaning phase. Only faecal pellets collected during the controlling phase were used for microhistological analysis. The faecal pellets analysed in this study were sampled during the study of Rehnus (2009). Faecal pellets were stored in a cold room at -20°C before conducting microhistological analysis.

For dietary analysis we selected the sampling sites with at least 2 faecal pellets for each season. There resulted 7 valid sampling sites. However, in order to have at least 10 samples per season (Homolka 1987; Katona and Altbäcker 2002), we randomly selected 4 different additional sampling sites per season. It was neither possible to know if the pellets collected belong to the same individual or to many individual nor the age or the sex of the individual.

Plant reference collection

An epidermis reference collection of the majority of the plants present in the study area was prepared following the procedure presented in Suter et al. (2004). Plants species were cut in small pieces and bleached in 2.5% sodium-hypochloride. After a while the epidermis could be removed and mounted on a microscope slide in glycerin, covered with a cover slip and sealed with polish nail. An identification key was created with these reference samples. References from the *Microscopic wood anatomy* (Schweingruber 1990) were used for woody fragments.

Faecal pellets analysis

We first processed the frozen pellets in an autoclave for 20 minutes at 120°C. Then, we randomly selected 2 pellets from each sample. The selected pellets were crushed in a mortar and mixed in a lab blender with water to allow the separation of each plant particle. The mixture was then rinsed through a sieve of 0.1 mesh widths and stored in 70% alcohol. For the analysis the mixture was transferred into a Petri dish and allowed to settle for 15 minutes. With a 2 ml pipette 10 random points were taken and mounted in a microscopic slide. Observations were made at 200x magnification. On each slide we identified 20 plant fragments systematically selected along almost two transects. The key criteria used for the identification were the form and size of the cell, the form and thickness of the cell wand, the form and size of stomata and the presence of trichomes. Most epidermal fragments were identified to the genus level and some of them to the species level. However, due to some deterioration or similarity between plant groups, most fragments were included in botanicals groups or category. Grasses were classified in two main groups according to the cell wand form. When identification was impossible, epidermal

fragments were classed as *unidentified*. Fragments with a surface smaller than 0.04 mm were not considered. Fragments were also classified according to the plant part (leaf or needle, bud, twig, bark, inflorescence or flower).

We totally identified 200 plant fragments for each sample (10 microscopic slides per sample and 20 epidermis fragments per slide) (Chapuis 1980). The first 10 samples were treated twice in order to avoid biases due to a method's habituation.

Data analysis

Results were expressed as relative frequency of plants species for each season (number of fragments per plant species or botanical groups divided by 2200, the total number of fragments observed each season).

To assess the seasonal variation of the diet we performed a Kruskall-Wallis's test for each species or botanical groups identified. Non-parametric statistics were preferred because of a non-normal distribution of the data and a small sample size (n = 11). In addition a Kruskall-Wallis test followed by a *post hoc* multiple comparison test performed using the Nemenyi-Damico-Wolfe-Dunn test (Hollander and Wolfe 1999) was computed for the categories *monocotyledons*, *forbs*, *dwarf shrubs*, *gymnosperms*, and *unidentified* as well as for the different plant parts.

Furthermore we conducted a Detrended Correspondence Analysis (Hill and Gauch 1980) using Canoco for Windows 4.5 (ter Braak and Smilauer 2002) to examine the basic difference between the seasons and to identify the main factor describing it. This method provides simultaneously an interpretable species and samples ordination (Hill and Gauch 1980). For this analysis we selected species and species groups respectively with a relative frequency of at least 5%. But in order to cover all the data, *Nardus stricta* and *other grasses* were combined to one group as well as *sedges* and *other monocotyledons* and *bryophytes* and *unidentified*. *Total dwarf shrubs* was used as a single variable.

To assess differences between seasons, axes scores from Axis 1 and Axis 2 were tested with a one-way ANOVA followed by a Fisher's Least-Significant-Difference Test for the seasons. All the univariate statistical analyses were performed in the statistical environment R version 2.8.1 (R Development Core Team 2008) complemented with the additional packages Coin version 1.0-9 (Hothorn et al. 2008).

Detrended Correspondence Analysis was furthermore employed to verify if the variation in the diet could be explained by the habitat type of the sampling site. Analyses were done for each season separately. Sampling sites were grouped according to the pine species present following HABITALP data (Lotz 2006).

Control

For the microhistological analysis we randomly selected two faecal pellets in each sample, which corresponds to the size of the smallest sample. In order to determine if the number of faecal pellets analysed influences the diversity of the results we computed supplementary analysis. For each season we selected a sample containing a great number of faecal pellets. Then, for each season, we performed microhistological analysis with 6 different mixtures composed from 1, 2, 3, 5, 10 and 15 faecal pellets (for winter only 4 with 1, 2, 5 and 10 faecal pellets). Results were expressed as a linear regression of the number of plant species identified on the number of faecal pellets analysed. Additionally a Pearson's correlations coefficient between the number of faecal pellets analysed and the number of plant species identified was calculated for each season.

Results

Within the 8800 fragments considered (2200 per season) 8038 fragments could be identified (91.34% of the total) and 762 fragments were classified as unidentified. The 8038 identified fragments are divided in 14 plant species, plant genera or botanical groups (Table 1).

Diet composition

On average the 44 samples analysed were composed of 47.00% gymnosperms and 32.47% monocotyledons, the remaining 11.88% consisting of dwarf shrubs (8.50%), forbs (2.81%) and bryophytes (0.57%), see Table 1.

Vegetative plant parts such as leaves and needles were the major components of the hare diet throughout the year, consisting on average of 79.80% of the fragments analysed. Buds, twigs, bark, stems, flowers and inflorescence were also consumed but in very low frequencies (Table 2).

Table 1 Number of fragments and relative frequencies of plant species identified in the 44 faecal samples from the 11 samples sites classified by plant group; species with relative frequencies lower than 1% are included in the class *Other* of each group (Tot = total, Un = unidentified and id = identified) Kruskall-Wallis p-value and significance levels are also presented (Sign. = significant, * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$).

Season	Autumn		Winter		Spring		Summer		*p-value*	Sign.
	Count	%	Count	%	Count	%	Count	%		
Nardus stricta	26	1.18	7	0.32	9	0.41	20	0.91	0.707	
Festuca sp.	259	11.77	73	3.32	128	5.82	149	6.77	0.333	
Grass 1[1]	165	7.50	73	3.32	232	10.55	213	9.68	0.038	*
Grass 2 [2]	117	5.32	22	1.00	61	2.77	62	2.82	0.024	*
Other grasses	69	3.14	9	0.41	34	1.55	85	3.86	0.010	**
Total grasses	636	28.91	184	8.36	464	21.09	529	24.05	0.024	*
Sedges	210	9.55	94	4.27	276	12.55	212	9.64	0.167	
Other monocotyledons[3]	72	3.27	25	1.14	89	4.05	66	3.00	0.086	
Tot. monocotyledons	**918**	**41.73**	**303**	**13.77**	**829**	**37.68**	**807**	**36.68**	**0.009**	**
Forbs	**73**	**3.32**	**1**	**0.05**	**44**	**2.00**	**129**	**5.86**	**0.000**	***
Erica carnea	53	2.41	109	4.95	50	2.27	21	0.95	0.048	*
Vaccinium myrtillus	12	0.55	13	0.59	32	1.45	16	0.73	0.899	
Other dwarf shrubs[4]	119	5.41	72	3.27	106	4.82	145	6.59	0.093	
Tot. dwarf shrubs	**184**	**8.36**	**194**	**8.82**	**188**	**8.55**	**182**	**8.27**	**0.935**	
Total dycotyledons	257	11.68	195	8.86	232	10.55	311	14.14	0.225	
Pinus sp.	591	26.86	1155	52.50	748	34.00	594	27.00	0.007	**
Un. gymnospermes	221	10.05	427	19.41	245	11.14	155	7.05	0.002	**
Tot. gymnospermes	**812**	**36.91**	**1582**	**71.91**	**993**	**45.14**	**749**	**34.05**	**0.003**	**
Bryophytes	24	1.09	22	1.00	1	0.05	3	0.14	0.311	
Un. epidermis	189	8.59	98	4.45	145	6.59	330	15.00	0.000	***
Tot. id. epidermis	2011	91.41	2102	95.55	2055	93.41	1870	85.00		
Tot. epidermis	2200	100.00	2200	100.00	2200	100.00	2200	100.00		

[1] *Deschampsia sp., Calamagrostis sp., Phleum sp., Poa sp.*

[2] *Anthoxanthum sp., Helitrichon sp., Trisetum sp., Koeleria pyramidata, Dactilis glomerata, Agrostis sp., Briza media*

[3] *Luzula sp*. and others unidentified monocotyledons

[4] *Rhododendron sp., Polygala sp., Vaccinium vitis-idaea* and others unidentified dwarf shrubs

Table 2 Number of fragments and relative frequencies of plant components identified in the 44 faecal samples from the 11 samples sites (Infl. = flowers and inflorescences, Leaf = leaves and needles). Kruskall-Wallis p-value and significance levels are also presented (Sign. = significant, * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$).

Season	Autumn		Winter		Spring		Summer		*p-value*	Sign.
	Count	%	Count	%	Count	%	Count	%		
Bark	16	0.73	17	0.77	7	0.32	2	0.09	0.020	*
Bud	89	4.05	223	10.14	92	4.18	70	3.18	0.008	**
Infl.	7	0.32	0	0.00	0	0.00	55	2.50	0.000	***
Leaf	1812	82.36	1694	77.00	1860	84.55	1656	75.27	0.005	**
Stem	19	0.86	13	0.59	36	1.64	16	0.73	0.368	
Twig	72	3.27	164	7.45	58	2.64	37	1.68	0.002	**
Unidentified	185	8.41	89	4.05	147	6.68	364	16.55	0.000	***
Total	2200	100.00	2200	100.00	2200	100.00	2200	100.00		

Seasonal variation

The diet selection of the Alpine mountain hare in the Swiss National Park varied throughout the year; the main differences were found between winter and the other seasons.

The consumption of gymnosperms (Kruskal-Wallis test: $\chi^2 = 14.130$, $df = 3$, $p < 0.01$) was significantly greater in winter than in autumn and summer (Nemenyi–Damico–Wolfe–Dunn test: $p < 0.01$), whereas the amount of monocotyledons (Kruskal-Wallis test: $\chi^2 = 11.589$, $df = 3$, $p < 0.01$) and forbs (Kruskal-Wallis test: $\chi^2 = 24.180$ $df = 3$, $p < 0.001$) consumed was significantly lower in winter then in the other seasons (Nemenyi–Damico–Wolfe–Dunn test: $p < 0.05$). The percentage of unidentified plant fragments found in the different samples also varied significantly throughout the year (Kruskal-Wallis test: $\chi^2 = 24.921$, $df = 3$, $p < 0.001$) and was greater in summer than in the other seasons (Nemenyi–Damico–Wolfe–Dunn test: $p < 0.05$) (Fig. 1). The amount of dwarf shrubs consumed is similar all year long. Only heather (*Erica carnea*), if considered alone, varied significantly (Kruskal-Wallis test: $\chi^2 = 7.925$, $df = 3$, $p < 0.05$).

The relative frequency of plant parts ingested also varied throughout the year. All the items tested, except the variable *Stem*, were significant (Kruskal-Wallis test: $df = 3$, $p < 0.01$). It resulted that inflorescences were only consumed in summer (Nemenyi–Damico–Wolfe–Dunn test: $p < 0.001$); the amount of bark, buds and twigs consumed varied significantly between winter and summer (Nemenyi–Damico–Wolfe–Dunn test: $p < 0.05$). Additionally the item *Bud* also varied between winter and autumn (Nemenyi–Damico–Wolfe–Dunn test: $p = 0.01$) and the item *Twig* between spring and winter (Nemenyi–Damico–Wolfe–Dunn test: $p < 0.05$). Leaf and needle consumption was significantly lower in summer and in winter than in spring (Nemenyi–Damico–Wolfe–Dunn test: $p < 0.05$) (Fig. 2).

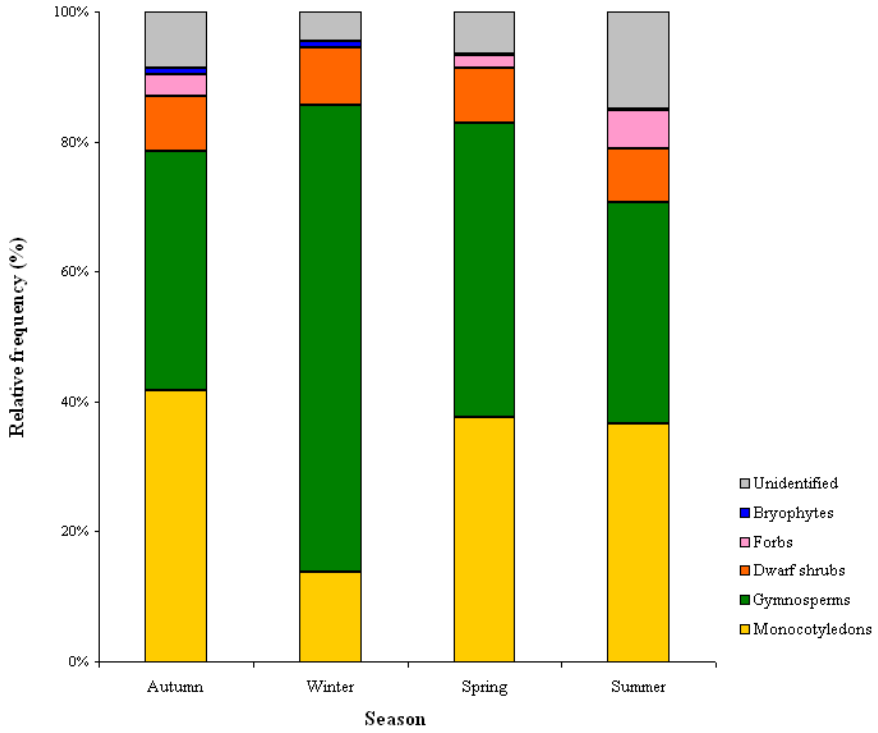

Fig. 1 Relative frequencies of occurrence of plant categories identified in the 44 samples analysed.

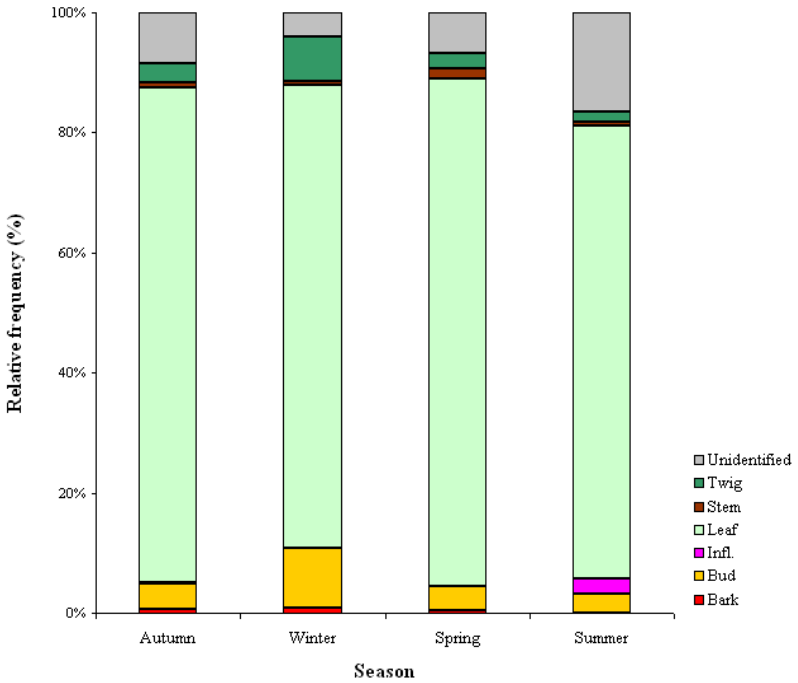

Fig. 2 Relative frequencies of occurrence of plant parts identified in the 44 samples analysed (Leaf = leaves and needles, Infl. = inflorescences).

Figure 3 shows the distribution of the samples (11 per seasons, total 44) and of the species composition along the two first axes. The first three axes explained 43.19% (Axis 1 = 31.58%, Axis 2 = 6.98% and Axis 3 = 4.63%) of the total variance in the data. Axis 1 was associated with the time of the year and explained how the diet composition differed between de seasons (ANOVA: F = 5.605, df = 3, $p < 0.01$); winter differed significantly from the other seasons (from autumn and summer: Fisher's Least-Significant-Difference test: $p = 0.001$ and from spring: Fisher's Least-Significant-Difference test: $p < 0.05$). Winter's samples were differentiated from the other samples by the high amount of pine (*Pinus sp*.) and unidentified gymnosperms. Axis 2 did not explain any variation in the data (ANOVA: $F = 1.331$, $df = 3$, $p > 0.05$), see Figure 4.

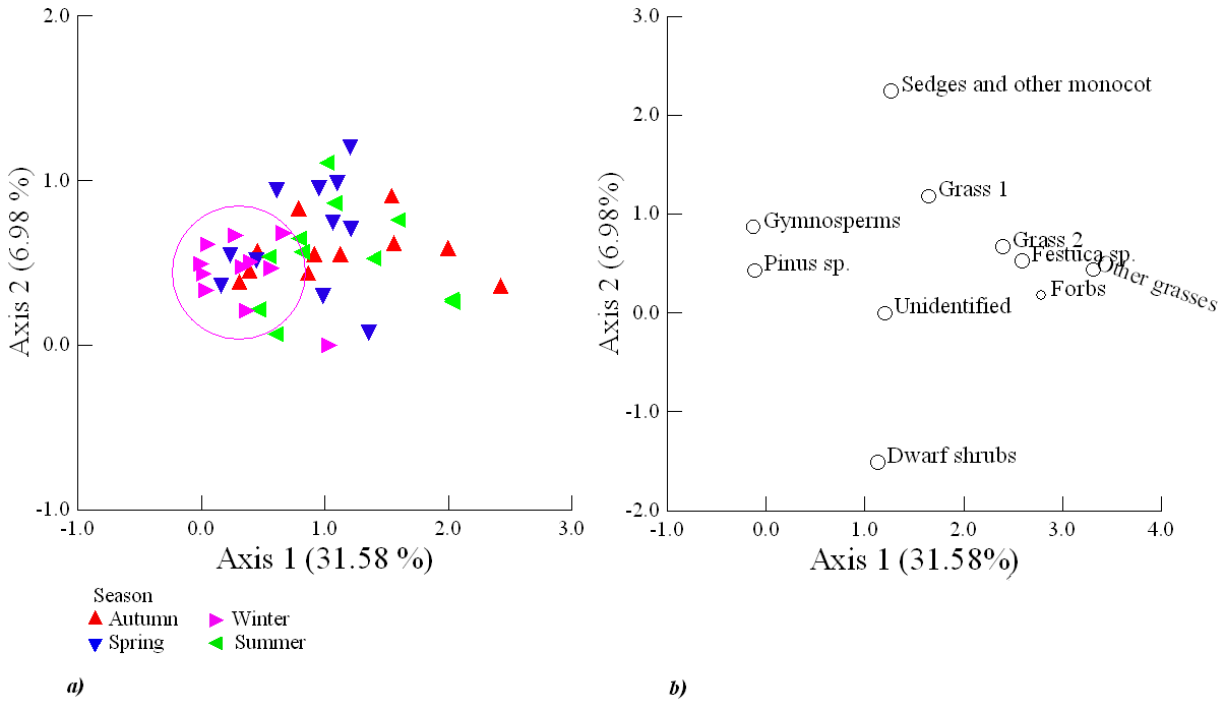

Fig. 3 Detrended Correspondence Analysis of ***a)*** the 44 samples of Alpine mountain hare's faecal pellets for the four seasons (n = 11 for each season) and ***b)*** of the 10 selected plant groups contained in the 44 faecal samples analysed (monocot = monocotyledons, Gymnosperms = unidentified gymnosperms).

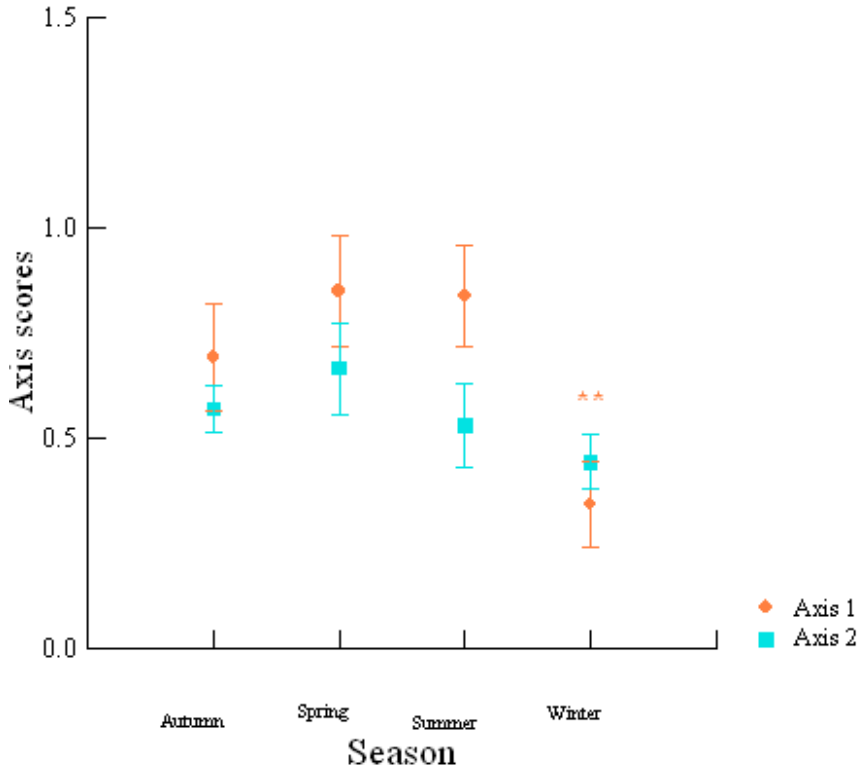

Fig. 4 Mean axes scores for the first two axis of the Detrended Correspondence Analysis for the four seasons, n = 11 for each season. Asterisks in the graph indicate significant differences ($p < 0.01$) between the seasons.

Variation between samples sites

The variation in the diet selection of the Alpine mountain hare observed in this study could not be explained by differences between the sampling sites. Figure 5 shows the distribution of the different sampling area groups and of the species composition along the two first axes for each season separately.

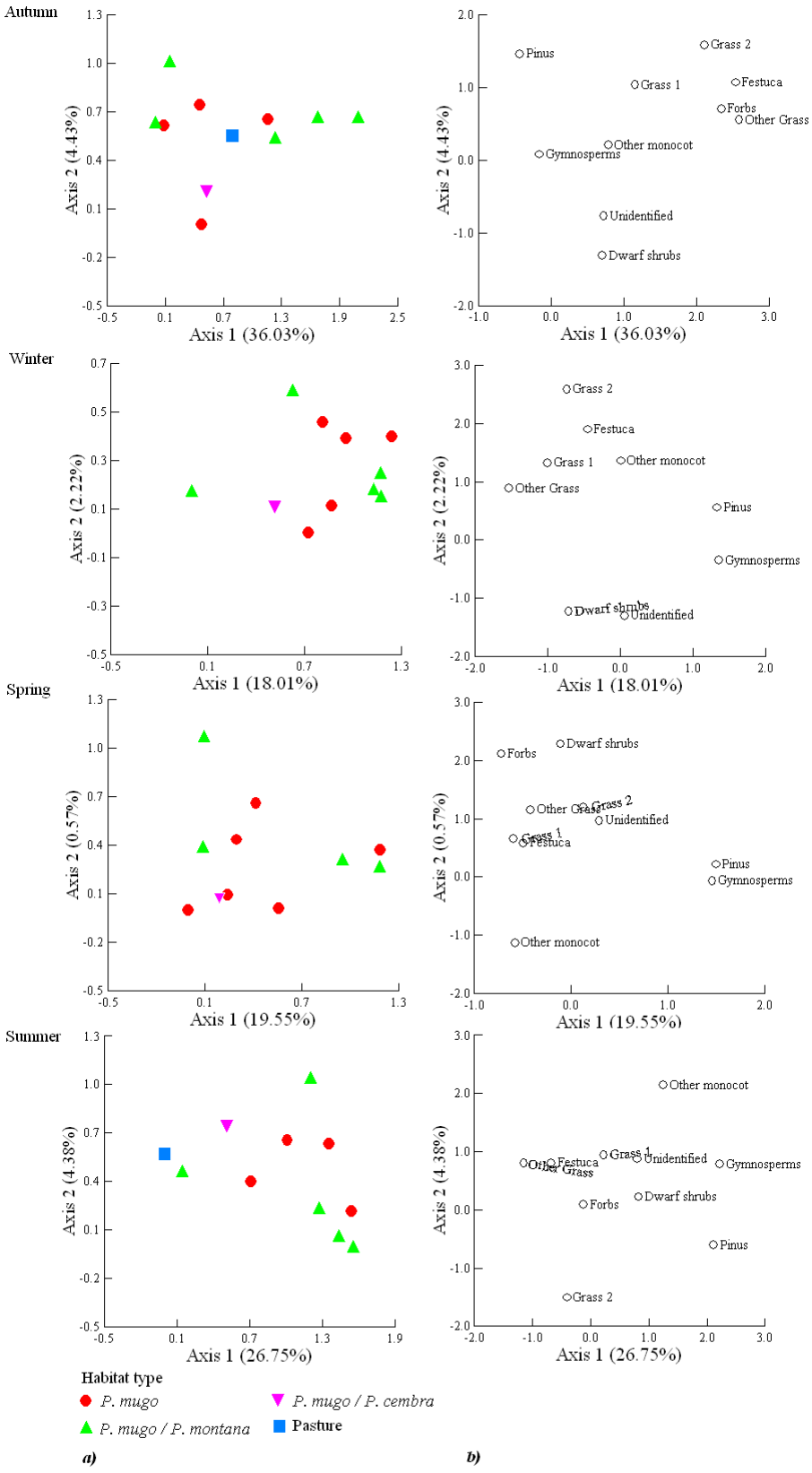

Fig. 5 Detrended Correspondence Analysis of ***a)*** the samples of Alpine mountain hare's faecal pellets for the four seasons grouped according to the habitat type (Lotz 2006) of the sampling sites and ***b)*** of the 10 selected plant groups contained in the samples analysed (monocot = monocotyledons, Gymnosperms = unidentified gymnosperms).

Control

The results from the autumn and summer samples show a very low correlation between the number of faecal pellets analysed and the number of plant species identified (Pearson's correlation coefficient *r*: autumn = -0.152, summer = 0.375). These correlation are higher for the spring and winter samples (Pearson's correlation coefficient *r*: winter = 0.995, spring = 0.841). Figure 6 shows the linear regression of the number of plant species identified on the number of faecal pellets analysed.

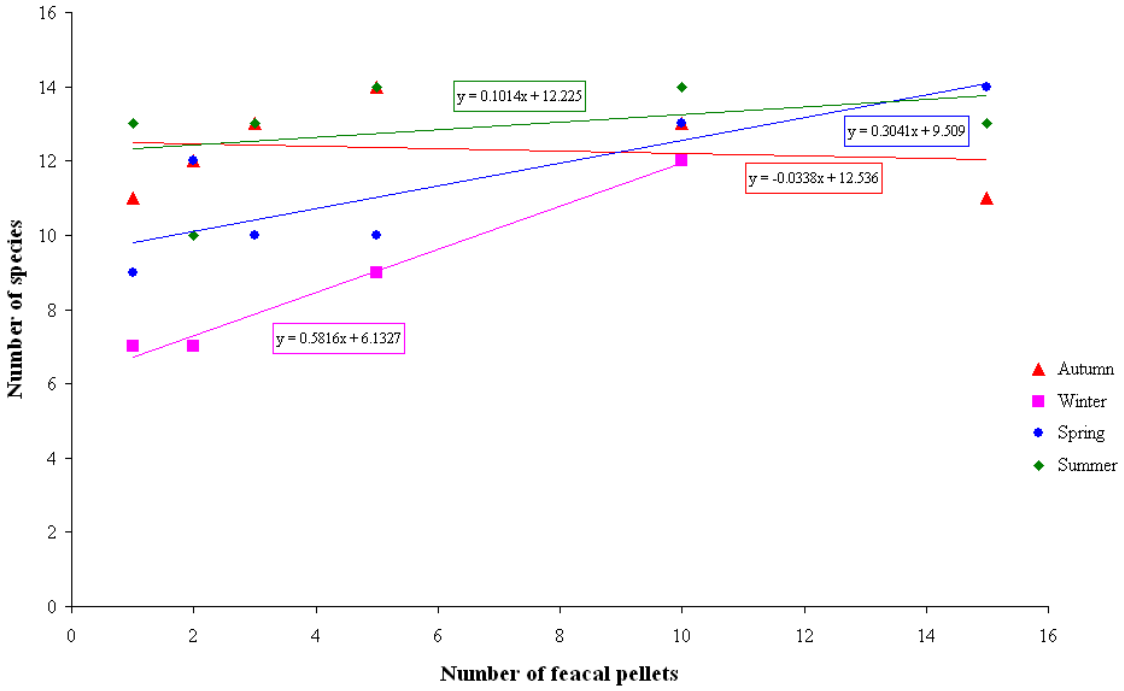

Fig. 6 Linear regression of the number of plant species identified on the number of faecal pellets analysed for each season. The equations of every slope are also presented.

Table 3 Annual averages of relative frequencies of plant groups and plant components identified in the diet of alpine mountain hare (*Lepus timidus varronis*) in different studies (ND = No data reported).

Authors	Bouche 1989	Loidl 1997	Present study
Study area	Écrins National Park (France)	Hohe Tauern National Park (Austria)	Swiss National Park (Switzerland)
Botanicals groups	Relative frequency (%)		
Monocotyledons	34.35	15.69	32.47
Gymnosperms	10.15	18.38	47.00
Dwarf shrubs	ND	48.28	8.50
Other dycotyledons	27.62	0.00	0.00
Forbs	ND	6.70	2.81
Total dycotyledons	27.62	54.98	11.31
Bryophytes	0.00	1.27	0.57
Broad leafed trees	0.00	9.71	0.00
Bark and buds	12.64	ND	5.86
Inflorescences	8.42	ND	0.70
Unidentified fragments	6.49	ND	8.66

Discussion

Several methods exist in order to investigate the diet of an herbivore. Chapuis (1980) analyze the main advantages and disadvantages of each technique. We selected the microhistological technique because it is an indirect method and therefore non-invasive. However this method is a non-quantitative method: it is not possible to quantify the correlation between ingested food items and items found in the faeces (Bouche 1989). Additionally this method tends to underestimate easily digestive plants like dycotyle forbs and young and reproductive plant parts, and overestimate hardly digestive plants like monocotyledons and gymnosperms (Putman 1984). Furthermore, some epidermises aren't characteristic enough to be determined to the species level. Although there are some methods to solve this problem, for the main analysis we choose to class the identified fragments in botanical category like *monocotyledons*, *forbs*, *dwarf shrubs*, *gymnosperms* and *bryophytes*. Additional fragments were classed in broader taxonomical groups according to the key epidermal characteristics and the frequency of occurrence in the faecal pellets analysed (Chapuis 1980). Concerning the number of faecal pellets required for a representative diet analysis, Chapuis (1980) observed that for the study of a lagomorph population present in a study site the number required is 5. In our study, considering the small sample size available, we used 2 faecal pellets, but we observed that the number of faecal pellets used has a small influence on the number of identified plant species. For autumn and summer samples, the linear regression doesn't show any influence of the number of faecal pellets analysis on the diversity of the result. This relation is higher in winter but this

result could be explained by the small sample size (n=4). A positive correlation between the number of faecal pellets analysed and the number of plant species identified is only present in the spring samples.

In this study the diet selection of the Alpine mountain hare varied significantly between winter and the other seasons. In general snow cover in winter largely reduces food availability and increases the difficulty of movement. Radio-tracking studies of Alpine mountain hare in subalpine ecosystems showed low activity rate and movements in winter, with home range size also smaller in this season, and this allows the animal to limit the energy spent (Gamboni 1997; Slotta-Bachmayr 1998; Nodari 2006; Genini-Gamboni et al. 2008). Moreover Alpine grasslands are generally avoided (Gamboni 1997; Nodari 2006). Snow cover is more important in grasslands than in forests and available food resources are scarce. In the present study coniferous trees are the winter primary food sources of Alpine mountain hare. In the study area Swiss mountain pine needles are the largest available food resource and pine apical bud represents a trophic resource with higher nutritive value largely available also in winter. Additionally food resources are coniferous twigs and bark. Winter feeding mainly based on coniferous parts was already described by Meile (1984).

In summer, besides monocotyledons and gymnosperms, Alpine mountain hare also consumed forbs and inflorescences. Forbs were consumed as well, at lower frequencies, in spring and autumn. This can indicate that when they are available Alpine mountain hare selects food items with higher nutritive value. Many studies on dietary requirements of leporids identified inflorescences and forbs in summer samples. This is generally associated with the higher nutritive value of forbs and of the reproductive plant parts (Homolka 1982; Chapuis 1990; Johannessen and Samset 1994; Wolfe et al. 1996; Paupério and Alves 2008).

Finally the percentages of dwarf shrubs consumed were similar for each season, only heather (*Erica carnea*) taken alone is significantly higher in winter.

Our results showed higher consumption frequencies of coniferous needles all year long but especially in winter. Coniferous needles, especially pine needles, are thickly and waxy plant parts and therefore their digestion can be relatively hard (Zahler and Khan 2003) and provides low energy intake. Additionally they contain secondary phytochemical compounds that can reduce digestibility of other ingested forage items (Adams et al. 1992) and reduce grown rate (Mole et al. 1990). The woolly flying squirrel (*Eupetaurus cinereus*) has been described as the only mammal feeding on pine needles as primary food source (Zahler and Khan 2003).

Inhabit coniferous woodland in summer, where food resources other than coniferous needles aren't abundant, could be an anti-predation behaviour. Forest assures better concealment and reduces predation risk. This strategy could also be a protection against climatic factors such as wind and sun. Radio-tracking studies on Alpine mountain hare reported a general avoidance of open pasture (Gamboni 1997; Nodari 2006). Results of Hik (1995) showed that snowshoe hares (*Lepus americanus*) feed on poor food items to

minimize predation risk. However Hodges and Sinclair (2003) doesn't find any evidence of a relationship between food quality and predation risk.

Alpine mountain hares, as well as all other lagomorph's species, are caecotrophe, which means that they reingest their own faeces for specific digestive purposes. They produce two types of faeces. The first type, the soft faeces, is rich in vitamins and microbial proteins, these faeces are reingested automatically at the excretion. The second type, the hard faeces are dry fibroses pellets composed mainly of poorly digestible food particle (Hirakawa 2001). Additionally, hard faeces reingestion (coprophagy) has been observed in many leporid species and also in Alpine mountain hare (Hirakawa 1997). Hard faeces reingestion helps leporid to survive in conditions of food scarcity and improves forage digestibility (Hirakawa 2001). Soft and hard faeces reingestion could also be seen as a defence against predation, because it allows to reduce the time spent in feeding (Gamboni 1997; Hirakawa 2001). Caecotrophy is considered as a digestive strategy equivalent to rumination (Hirakawa 2001) and it may help Alpine mountain hare to exploit hardly digestible trophic resources like coniferous needles.

This study tends to confirm the results of other studies on mountain hare which showed that this species is a generalist herbivore feeding on available food items and capable of consuming a wide range of plant species (Johannessen and Samset 1994; Tangney et al. 1995; Hiltunen 2003; Rao et al. 2003*b*).

Mammals of the genus *Lepus* are herbivores with an intermediate feeding strategy. They can switch between grazing (monocotyledons, forbs) and browsing (twigs and bark) (Hulbert et al. 2001). Intermediate feeding strategy is well known in North Europe where winter food consists mainly of twigs and bark from dycotyledons trees (Hiltunen 2003; Hjalten et al. 2004). However, in the present study this strategy is less observed: in summer, autumn and spring Alpine mountain hare are mainly grazers consuming monocotyledons and dycotyledons and in winter they switch on a diet mainly composed of gymnosperm's needles.

Compared to our study, the results of previous studies on Alpine mountain hare diet are relatively different. In the Hohe Tauern National Park (Austria) dwarf shrubs were the main component of Alpine mountain hare's diet and gymnosperm were consumed as well in high percentage throughout the year (Loidl 1997), while in the Écrins National Park (France) monocotyledons, mainly fescues, were the most frequent items, commonly consumed also in winter; gymnosperms were seldom found and mainly in winter (Bouche 1989), see also Table 3. These differences can be explained by the differences between the habitat type.

According to this study, both previous studies on Alpine Mountain hare (Bouche 1989; Loidl 1997) underline a greater amount of unidentifiable plant fragments in summer. This tendency is also found in the study on the Iberian hare (Paupério and Alves 2008). In summer the diversity and the amount of available food items is greater than in the other seasons. Moreover forbs are often unidentifiable because of damages incurred during the digestive process.

With this study we have an insight of the diet of the Alpine mountain hare in a subalpine ecosystem over the course of a year. Samples collected above the timberline weren't enough to obtain representative results on the diet of Alpine mountain hare in an alpine ecosystem. However, it could be interesting to complete the sampling in order to enlarge the study area and compare Alpine mountain hare diet in a subalpine and in an alpine ecosystem. It would also be important quantify the correlation between available and selected food items to investigate diet selection.

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