



Research Article

Seasonal changes in habitat use and feeding strategy of the mountain hare (*Lepus timidus*) in the Central Alps

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Keywords:

habitat selection
diet analysis
feeding
dung
mountain pine shrubs

Article history:

Received: 1 September 2011

Accepted: 4 February 2013

Acknowledgements

We would like to thank the Swiss National Park for permission to conduct the study; Philippe Küpfer for his motivated help in plant identification; all helpers, field workers, computer- and software supporters and Georg Gratzler for helpful comments on a previous draft of the manuscript; Matt W. Hayward and other anonymous reviewers for providing constructive and insightful comments on this manuscript.

Abstract

The mountain hare *Lepus timidus* (Linnaeus, 1758) is one of the smallest mammals in Alpine environments that stays active year-round without any conspicuous physiological adaptations. Mountain hares thus need to respond to seasonal changes by adaptive habitat and diet choice. We studied seasonal changes in habitat use and feeding strategy in the continental Central Alps during one year. Monitoring of the presence and density of dung and microhistological analysis of faecal pellets revealed that forest habitats, particularly mountain pine shrubs (*Pinus mugo* ssp.), were used throughout the year, whilst open habitats were avoided during snow-covered seasons. The probabilities of pellet presence and density were positively correlated with the proportion of trees and grass in spring, summer and autumn whereas in winter, they correlated only with the proportion of trees. The observed patterns can be explained by the importance of shelter and food availability which change seasonally and especially due to snow cover. We concluded that the availability of shelter was more important than food because hares selected habitat types that offered security from predators rather than habitat types with high food quality.

Introduction

The mountain hare (*Lepus timidus*) lives at elevations from 1300 to 3500 m a.s.l. in the Alps and is active throughout the year (Angerbjörn and Flux, 1995; Thulin and Flux, 2003; Nodari, 2006). To cope with the extreme seasonal changes in climate and resource availability in its alpine environment, especially in winter it does not physiologically adapt as other alpine species do. Small mammals usually cope with this twofold challenge with daily torpor or hibernation (Ruf and Arnold, 2000). Large mammals, such as ungulates, are capable of withstanding long, cold winters with low food availability by excellent fur insulation and counter current heat exchange mechanisms contributing to minimize energy requirements under cold load, nocturnal hypometabolism (Arnold et al., 2004, 2006), and long distance movements (Zweifel-Schielly et al., 2009). A strategy for the mountain hare to respond to seasonal changes might be adaptive habitat and diet choice. It copes with harsh environmental conditions by minimizing its home range size (Gamboni, 1997; Slotta-Bachmayr, 1998; Nodari, 2006), and using a flexible foraging and nutritional strategy which allows the use of low-quality food (Loidl, 1997; Iason and Van Wieren, 1999; Hirakawa, 2001; Hulbert et al., 2001). This results in the reduction of the metabolic rate instead of depleting body reserves (Pyörnilä et al., 1992; Thulin and Flux, 2003; Nieminen and Mustonen, 2008; Rehnus et al., 2010).

In forested environments, habitat selection by hares can be explained by the availability of shelter and food plants (Wolff, 1980; Pehrson and Lindlöf, 1984; Hewson and Hinge, 1990; Hulbert et al., 1996; Hiltunen et al., 2004; Nodari, 2006). Habitats with high shelter availability limit direct visual contacts of predators to hares and/or give it a high chance

to flee from them. Furthermore, the undergrowth in these habitats decreases wind speed and consequently helps to reduce heat loss for the animals (Grace and Easterbee, 1979). The mountain hare can be classed as an intermediate feeder (Hulbert et al., 2001) and its foraging strategy depends on the regional food resource availability. In Scandinavia, summer diet is composed of different grass and forb species (Johannessen and Samset, 1994) while in Scotland the hare switches from a high consumption of grass in summer to a diet principally composed of common heather (*Calluna vulgaris*) in winter (Hulbert et al., 2001; Rao et al., 2003).

Seasonal changes in climate and resource availability in the continental Central Alps are extreme and little is known about how the alpine mountain hare copes with such seasonal changes with regard to its habitat and resource use. We hypothesized that habitat selection and preference for plant species as food resource will be an important mechanism to cope with the changing environmental conditions. To this end, we studied i) the habitat type selection per season; ii) the seasonal importance of habitat composition variables; and iii) number of fragments and relative frequencies of used plant species.

Material and methods

Study area

The study area was situated along the Ofenpass in the Swiss National Park (SNP) in southeastern Switzerland (46° 39' N, 10° 11' E; Fig. 1). The investigated elevation ranges from 1660 to 2580 meters a.s.l. and the area consists of mainly nine habitat types: scree slopes (33%), rocks (17%), meadows (16%); mixed grasses including *Nardus stricta*, *Festuca* sp., *Poa* sp., *Agrostis* sp., *Luzula* sp., and sedges), timber stands (11%), sapling stands (9%); dominated by *Pinus mugo* ssp.), storeyed stands (7%); mixed by *Larix decidua*, *Pinus cembra*, *Pinus sylvestris*,

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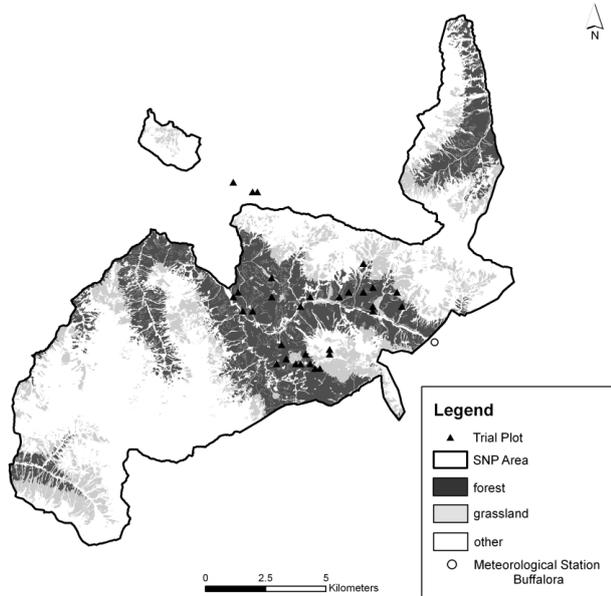


Figure 1 – Study area showing dung plots and the meteorological station Buffalora.

Pinus mugo ssp., *Larix decidua*, *Picea abies*), pole timber (2%), rills (2%), mature stands (1%) and other habitats (2%) (Lotz, 2006). The climate in the park is continental. The observed mean precipitation between 1961-1990 in January is 54 mm; in July, it is 104 mm, measured at the Parks weather station at Buffalora (1970 m a.s.l.). The mean temperatures are -9.2° C in January and 10.3° C in July (Aschwanden et al., 1996).

Habitat analysis

Habitat selection by mountain hares was assessed by observation of dung presence and density. Counts of the hare dung provide a quick and more cost- and time-effective method of tracking hare abundance (Litvaitis et al., 1985; Krebs et al., 2001). Despite some drawbacks, such as pellet clumping and pellet loss (Krebs et al., 2001; Murray et al., 2002; Hodges and Mills, 2008), faecal pellet counting can provide an index of habitat use by hares (*L. timidus*, Angerbjörn 1983; Hiltunen and Kauhala 2006; *L. americanus*, Litvaitis et al. 1985; Murray et al. 2005). A recent study suggests using plot sizes ranging from 0.1 to 1 m² for pellet surveys of snowshoe hares (Hodges and Mills, 2008) but the therein described high hare densities cannot be found in the Alps (Gamboni, 1997; Slotta-Bachmayr, 1998; Nodari, 2006). Instead, we used larger quadrats of 400 m² (20 × 20 m) because hare density was unknown for our study area (but expected lower than in North America) and home range sizes in alpine regions seem to be highly variable (Gamboni, 1997; Slotta-Bachmayr, 1998; Nodari, 2006).

We preselected the location of plots using a GIS in a grid of approximately 200 m and plot locations were selected choosing in the main habitat types of the SNP and in their elevation ranges (minimum three plots per habitat type, installed in low, middle and high altitude, respectively). Rocky habitats were deemed unsuitable habitat for hares (Nodari, 2006) and thus excluded from the study. Dung monitoring was carried out on the 31 installed plots (winter: n = 28, spring: n = 27, summer: n = 31, autumn: n = 31) between 2007-2008. Plot accessibility in winter and spring (danger of avalanches) was taken into consideration during the selection of the plots. Nevertheless, it was not possible to observe seven of the plots (one scree plot in spring and all rill habitats in winter and spring) due to the high risk of avalanches.

First, we cleared the plots of all mountain hare dung. Three nights later, plots were revisited and dung was counted. For each plot, habitat type and its detailed habitat composition (proportion of rock, scree, grass, dwarf shrub and tree cover) was determined. Table 1 shows the selected habitat types and the changes in their separate habitat composition across seasons (sum of % vegetation layer per habitat type and

Table 1 – Changes in proportion of vegetation layers per habitat type across seasons (% mean±SE).

Habitat type	Scree	Grass	Dwarf shrubs	Trees	Snow
<i>Spring</i>					
Meadow	0±0	37±19	10±10	0±0	53±26
Scree	33±33	13±9	0±0	0±0	54±29
Sapling stand	0±0	23±7	7±3	70±6	0±0
Pole timber	0±0	13±3	17±9	63±3	7±7
Timber stand	0±0	37±12	17±9	43±9	3±3
Mature stand	0±0	53±13	10±6	30±6	7±7
Storeyed stand	0±0	24±3	27±5	48±4	1±1
<i>Summer/Autumn</i>					
Meadow	13±9	77±12	10±10	0±0	0±0
Rills	73±17	17±12	10±6	0±0	0±0
Scree	83±8	15±5	0±0	0±0	0±0
Sapling stand	0±0	23±7	7±3	70±6	0±0
Pole timber	0±0	17±7	20±6	63±3	0±0
Timber stand	0±0	40±15	17±9	43±9	0±0
Mature stand	0±0	60±12	10±6	30±6	0±0
Storeyed stand	3±2	24±3	27±5	46±4	0±0
<i>Winter</i>					
Meadow	0±0	0±0	0±0	0±0	100±0
Scree	3±3	0±0	0±0	5±5	92±5
Sapling stand	0±0	0±0	0±0	47±9	53±9
Pole timber	0±0	±0±0	0±0	53±7	47±7
Timber stand	0±0	0±0	0±0	43±9	57±9
Mature stand	0±0	0±0	0±0	30±6	70±6
Storeyed stand	0±0	3±3	1±1	40±4	56±7

season = 100%). For example, we found different levels of snow cover on the investigated plots in winter (all plots with snow cover; height of snow 65.3±5.2 cm) and spring (five plots with snow cover; height of snow 6.5±3.0 cm) only depending on their habitat type (Tab. 1).

Analyses of long term observations by park rangers between 1979 and 2006 (unpublished data) and hunting statistics in the nearby hunting district (Denoth 2006, pers. comm.) showed that the mountain hare is allopatric from the European hare (*Lepus europaeus*) in the study area. This minimized the probability that our sampled dung have been confused with similar dung of the European hare. Furthermore, predators can be an important factor which affects the habitat selection by hares (Wolff, 1980; Hewson and Hinge, 1990; Hiltunen et al., 2004). However, in our study area predator density, such as of fox (*Vulpes vulpes*) and Golden eagle (*Aquila chrysaetos*), is equally distributed (Haller 2006, pers. comm.) and might therefore not bias the results.

Table 2 – Seasonal model selection (winter: n = 28; spring: n = 27; summer: n = 31 and autumn: n = 31) for the density of dung in relation to environmental covariates with ΔAICc values < 2. K = number of parameters, LogL = maximized log-likelihood, w = AICc weight.

Variables in model	K	LogL	ΔAICc	w
<i>Spring</i>				
trees	3	34.927	0	0.129
.	2	33.286	0.739	0.089
trees+preci	4	35.836	0.958	0.080
dwarf+snow	4	35.813	1.003	0.078
snow	3	34.416	1.022	0.077
trees+dwarf	4	35.626	1.376	0.065
dwarf+snow+preci	5	36.903	1.861	0.051
<i>Summer</i>				
.	2	19.979	0	0.172
trees	3	21.155	0.110	0.163
scree	3	20.599	1.221	0.093
dwarf	3	20.222	1.975	0.064
<i>Autumn</i>				
dwarf	3	50.276	0	0.160
.	2	49.017	0.059	0.155
grass+dwarf	4	50.824	1.554	0.073
scree	3	49.486	1.581	0.072
<i>Winter</i>				
.	2	39.922	0	0.454

Diet analysis

For dietary analysis we selected pellets from plots with at least two pellets for each season (valid for seven plots). In order to have at least 10 samples per season (Homolka, 1987; Katona and Altbäcker, 2002), we randomly selected four different additional plots per season.

To identify the used plant species, an epidermis reference collection of the majority of the plants present in the study area and microhistological analysis of the fresh pellets (not older than three days) followed the procedure described in Suter et al. (2004). Microhistological analysis may produce biased results because this method tends to underestimate easily digestive plants like dycotyle forbs, young and reproductive plant parts, and overestimate hardly digestive plants like graminoids and gymnosperms (Putman, 1984). Therefore, fragments were classed in broader taxonomical groups according to the key epidermal characteristics and the frequency of occurrence in the pellets analysed (Chapuis, 1990). For the main analysis we classed the identified fragments in five botanical category (graminoids, forbs, dwarf shrubs, gymnosperms and bryophytes). When identification was impossible, epidermal fragments were classed as unidentified. In total, 200 plant fragments for each sample (10 microscopic slides per sample and 20 epidermis fragments per slide) were identified (Chapuis, 1990). The first 10 samples were tested two times to avoid biases due to a method's habituation.

Considering the small sample size available, we used two pellets although Chapuis (1990) stated that a minimum of five pellets is required for a representative diet analysis. Beforehand, we tested the effect of number of pellet analysed on the diversity of the results and could not find a significant influence.

Data analysis

For habitat analysis we used a two-scale approach. In a first step, we calculated the Jacobs' index to describe the preference/avoidance of habitat types per season based on presence of dung. In the second step, we applied model selection to analyse the influence of habitat composition on the presence of hares and density of dung within each season. Additionally, we analysed the results of the plant species composition of seasonal dung samples.

Habitat type selection

Seasonal habitat selection was studied using a selection index that measures whether one habitat type is preferred, avoided or used as expected based on habitat availability. We chose the Jacobs' index be-

cause it minimizes problems associated with electivity (e.g., same relative abundance of available resources; Jacobs 1974):

$$D = \frac{r - p}{r + p - 2rp} \quad (1)$$

where r is the proportion of the total number of plots for a given habitat type during a season and p is the proportion of the total number of investigated plots of that habitat type in the study area. The resulting value ranges from +1 to -1, where +1 indicates maximum preference and -1 maximum avoidance (Jacobs, 1974).

Habitat composition

Density of dung (calculated dung per square meter) were analysed per season using logistic regression in R, version 2.8.1 (R Development Core Team, 2010). Density was modelled as a function of plot composition, the proportion of scree, grass, dwarf shrub and tree cover, and precipitation. Composition variables changed between seasons because of missing observations within a season as follows: spring (grass, dwarf shrub, tree, and snow), summer/autumn (scree, grass, dwarf shrubs, and trees) and winter (trees and snow). Explanatory variables were z-standardized and log-transformed (if necessary). At all seasonal levels, additive models of all possible combinations of covariates were examined.

We used model selection following Burnham and Anderson (2002) to evaluate which of the considered models were supported by the field data. Due to the low sample size, Akaike Information Criterion (AICc = AIC with a correction for finite sample sizes) and Akaike weight (w) were used for comparing the different models (Johnson and Omland, 2004). Models with $\Delta AICc$ values < 2 were considered to be equivalent, and the simplest model with the lowest AICc was selected (Burnham and Anderson, 2002). Furthermore, Akaike weights were calculated to indicate the level of support of a given model relative to all models in the candidate model set (Burnham and Anderson, 2002). Parameter estimates and associated SE were then calculated by model-averaging across the models for which the sum of the Akaike weights was > 95%.

Diet analysis

To assess the seasonal variation of the diet we performed a Kruskal-Wallis's test for each species or botanical group identified. Non-parametric statistics were preferred because of the non-normal distribution of the data and a small sample size ($n = 11$). In addition, a post hoc multiple comparison test was performed using the Nemenyi-Damico-Wolfe-Dunn test (Hollander and Wolfe, 1999) for the categories graminoids, forbs, dwarf shrubs, gymnosperms, and unidentified.

Results and discussion

Habitat type selection

The mountain hares selected mountain pine shrubs during all seasons (annual mean $D = 0.21 \pm 0.04$, $n = 12$) while the proportion of other selected habitats varied (Fig. 2) between seasons. Forest habitats are known to be exploited by the mountain hare for shelter and food throughout the year. Observations suggest that old forests do not provide sufficient shelter and food for hares (Lindlöf et al., 1974) and instead, mountain pine shrubs are preferred (Hiltunen and Kauhala, 2006; Nodari, 2006). Habitats without forest cover were only preferred during summer and mostly avoided during periods with snow-cover (Fig. 2). This pattern is consistent with results from both alpine and non-alpine studies (Hewson and Hinge, 1990; Gamboni, 1997; Slotta-Bachmayr, 1998; Dahl, 2005; Nodari, 2006). During summer, meadows were selected because they represent important food sources. The hares make short forays in the meadows and return afterwards to sheltered sites inside forest.

Habitat composition

Dung density of mountain hares varied significantly across seasons ($F_{3,113} = 3.84$, $p = 0.012$) and were highest in summer (0.10 ± 0.02), followed by spring (0.05 ± 0.01), autumn (0.04 ± 0.01 , $p = 0.049$ compared to summer), and winter (0.03 ± 0.01 , $p = 0.012$ compared to

Table 3 – Parameter estimates and associated SE were calculated for the density of dung by model-averaging across the models for which the sum of the Akaike weights was > 95% within a season.

	Model-averaged parameter (estimate \pm SE)
<i>Spring</i>	
Proportion of grass	0.00 \pm 0.02
Proportion of trees	0.03 \pm 0.02
Precipitation	-0.02 \pm 0.01
Proportion of dwarf	-0.02 \pm 0.02
Proportion of snow	-0.03 \pm 0.02
<i>Summer</i>	
Proportion of grass	0.00 \pm 0.03
Proportion of trees	0.04 \pm 0.04
Precipitation	0.01 \pm 0.02
Proportion of scree	-0.01 \pm 0.04
Proportion of dwarf	0.01 \pm 0.03
<i>Autumn</i>	
Proportion of grass	0.16 \pm 0.09
Proportion of trees	0.08 \pm 0.09
Precipitation	0.02 \pm 0.07
Proportion of dwarf	-0.03 \pm 0.08
Proportion of scree	-0.15 \pm 0.10
<i>Winter</i>	
Proportion of snow	0.00 \pm 0.02
Proportion of trees	0.10 \pm 0.07
Precipitation	-0.18 \pm 0.10

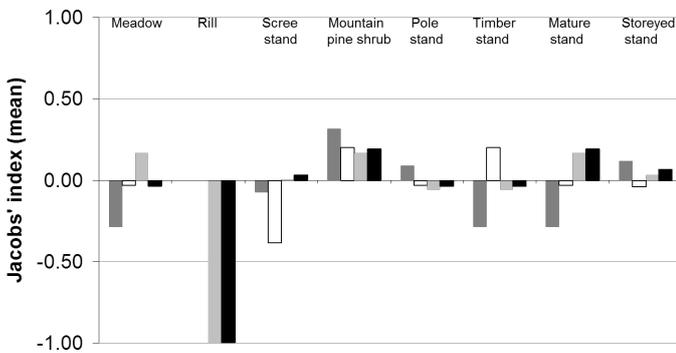


Figure 2 – Jacobs' index (mean per season) of mountain hare selection for habitat type in winter (n = 28; dark gray), spring (n = 27; white), summer (n = 31; light gray) and autumn (n = 31; black). The resulting value ranges from +1 to -1, where +1 indicates maximum preference and -1 maximum avoidance (Jacobs, 1974).

summer). Observed seasonal changes in habitat usage throughout the year (Fig. 2) corresponded with telemetric studies of mountain hares in the Alps (Gamboni, 1997; Slotta-Bachmayr, 1998; Nodari, 2006). The highest dung density across different plots and the highest concentration of dung within the plots coincided with the higher home range use by hares in summer (Gamboni, 1997; Slotta-Bachmayr, 1998; Nodari, 2006)s availability of high quality food and with the reproductive period of the mountain hare when a higher number of hares in the study area was assumed. The lowest number of plots with dung presence and the lowest dung density per plot could be explained by the absence of reproduction, limited food availability, coupled with annual peaks in mortality, and reduced metabolism in winter. However, in snow cover periods, access to some plots was limited. On the other hand, problems in detecting the dung in the snow were reduced by short-term collection and thus by sampling during similar weather conditions (mostly without snow fall between the first and the second visit).

We found that the variables influencing the dung density varied with season (Tables 2 and 3). The influence of trees on the density of dung was higher than of grass and other variables. This may be explained

by the availability of shelter in trees and high quality food plants in grass (depending on snow-cover), all of which influences the habitat choices of the hares (Wolff, 1980; Pehrson and Lindlöf, 1984; Hewson and Hinge, 1990; Hulbert et al., 1996; Hiltunen et al., 2004). Undergrowth decreases heat loss for the animals (Grace and Easterbee, 1979) and direct visual contacts of predators. We assume that habitats providing shelter and sufficient food, help to minimize energy requirements under cold load and indicated hypometabolism (Pyörnilä et al., 1992; Rehnus et al., 2010). It was also observed that winter precipitation could affect the density of pellets (Tab. 3), presumably because reduced activity by hares during harsh weather condition reduced food uptake and thus pellet production. On the other hand snow can have a positive influence on food uptake by facilitating the access to the tree shoots.

Diet analysis

Among the 8800 fragments contained in 44 samples (2200 per season), 8038 fragments could be allocated to species (91.3% of the total) while 762 fragments (8.7%) were classified as unidentified (Tab. 4). A total of 14 plant species were identified. On average, the 44 samples analysed were composed of 47.0% gymnosperms, 32.5% graminoids and the remaining 11.9% consisting of dwarf shrubs (8.5%), forbs (2.8%) and bryophytes (0.6%). The plant selection of the mountain hare varied throughout the year; the main differences were found between high snow-covered and non- and low snow-covered 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 graminoids (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 compared to the other seasons (Nemenyi–Damico–Wolfe–Dunn test: $p < 0.05$). This indicates that the mountain hare prefers food items with higher nutritive value when they are available. Many studies on dietary requirements of leporids observed a selection of inflorescences and forbs in summer samples because these are generally associated with an higher nutritive value (Chapuis, 1990; Homolka, 1982; Johannessen and Samset, 1994; Paupério and Alves, 2008; Seccombe-Hett and Turkington, 2008; Wolfe et

Table 4 – Number of fragments (Freq.) and relative frequencies (%) of plant species identified in the 44 faecal samples from the 11 samples sites classified by botanical group; species with relative frequencies lower than 1% are included in the class *Other* of each group (*Tot* = total, *Un* = unidentified and *id* = identified). Kruskal-Wallis *p*-value and significance levels are also presented (*Sign* = significant, * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$).

Botanical group	Spring		Summer		Autumn		Winter		<i>p</i> -value	Sign
	Freq.	%	Freq.	%	Freq.	%	Freq.	%		
<i>Nardus stricta</i>	9	0.4	20	0.9	26	1.2	7	0.3	0.707	
<i>Festuca</i> sp.	128	5.8	149	6.8	259	11.8	73	3.3	0.333	
Grass 1 ¹	232	10.6	213	9.7	165	7.5	73	3.3	0.038	*
Grass 2 ²	61	2.8	62	2.8	117	5.3	22	1.0	0.024	*
Other grasses	34	1.6	85	3.9	69	3.1	9	0.4	0.010	*
Total grasses	464	21.1	529	24.1	636	28.9	184	8.4	0.024	*
Sedges	276	12.6	212	9.6	210	9.6	94	4.3	0.167	
Other graminoids ³	89	4.1	66	3.0	72	3.3	25	1.1	0.086	
Tot. graminoids	829	37.7	807	36.7	918	41.7	303	13.8	0.009	**
Forbs	44	2.0	129	5.9	73	3.3	1	0.1	<0.001	***
<i>Erica carnea</i>	50	2.3	21	1.0	53	2.4	109	5.0	0.048	*
<i>Vaccinium myrtillus</i>	32	1.5	16	0.7	12	0.6	13	0.6	0.899	
Other dwarf shrubs ⁴	106	4.8	145	6.6	119	5.4	72	3.3	0.093	
Tot. dwarf shrubs	188	8.6	182	8.3	184	8.4	194	8.8	0.935	
Total dycotyledons	232	10.6	311	14.1	257	11.7	195	8.9	0.225	
<i>Pinus</i> sp.	748	34.0	594	27.0	591	26.9	1155	52.5	0.007	**
Un. gymnospermes	245	11.1	155	7.1	221	10.1	427	19.4	0.002	**
Tot. gymnospermes	993	45.1	749	34.1	812	36.9	1582	71.9	0.003	**
Bryophytes	1	0.1	3	0.1	24	1.1	22	1.0	0.311	
Un. epidermis	145	6.6	330	15.0	189	8.6	98	4.5	<0.001	***
Total id. epidermis	2055	93.4	1870	85.0	2011	91.4	2102	95.6		
Total epidermis	2200	100.0	2200	100.0	2200	100.0	2200	100.0		

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

² *Anthoxanthum* sp., *Helitrichon* sp., *Trisetum* sp., *Koeleria pyramidata*, *Dactylis glomerata*, *Agrostis* sp., *Briza media*.

³ *Luzula* sp. and others unidentified graminoids.

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

al., 1996). Graminoids are available on grass sites areas without shelter against predators. Results of Hick (Hick, 1995) showed that snowshoe hares feed on poor food items to minimize predation risk. On the other hand, Hodges and Sinclair (2003) did not find any evidence of a relationship between food quality and predation risk. For mountain hares, reduction of predation risk and intake of high food quality might lead to a trade-off behaviour. The uptake frequency of coniferous needles was high in winter (Tab. 4) which is in contrast with the results by Hjalten et al. (2004) who showed that mountain hares generally preferred deciduous plant species in winter avoiding conifers. However, in our study area the availability of deciduous plants was low. Coniferous needles, especially pine needles, are thick and waxy plant parts, that are relatively difficult to digest (Zahler and Khan, 2003) and provide only low energy. Additionally, they contain secondary phytochemical compounds that can reduce digestibility of other ingested forage items (Adams et al., 1992) and reduce growth rate (Mole et al., 1990). Such patterns illustrate the flexibility of the mountain hare in its feeding strategy which depend on the regional availability of food resources and predation pressure.

This study shows, in accord with results from other investigations (Hiltunen, 2003; Johannessen and Samset, 1994; Rao et al., 2003; Tangney et al., 1995; Loidl, 1997), that the mountain hare seems to be a generalist herbivore capable to adapt its diet to the environment. However, flexible foraging strategy permits survival and production through periods of changing or unpredictable forage quality and availability.

Finally, we concluded that the availability of shelter was more important than food because hares selected habitat types that offered security from predators rather than habitat types with high food quality. Furthermore the occurrence of a suitable mix of different habitat for the mountain hares' reaction to changing environmental conditions in surrounding areas (heterogeneity of habitats) should be considered in management of the mountain hare population. ☺

References

- Adams D.C., Pfister J.A., Short R.E., Cates R.G., Knapp B.W., Wiedmeier R.D., 1992. Pine Needle Effects on *in vivo* and *in vitro* Digestibility of Crested Wheatgrass. *J. Range Manage.* 45: 249–253.
- Angerbjörn A., 1983. Reliability of pellet counts as density estimates of mountain hares. *Riistatieteellisiä Julkaisuja* 41: 13–20.
- Angerbjörn A., Flux J.E.C., 1995. *Lepus timidus*. *Mamm. Spec.* 0(495): 1–11.
- Arnold W., Ruf T., Kuntz R., 2006. Seasonal adjustment of energy budget in a large wild mammal, the Przewalski horse (*Equus ferus przewalskii*) II. Energy expenditure. *J. Exp. Biol.* 209(22): 4566–4573.
- Arnold W., Ruf T., Reimoser S., Tataruch F., Onderscheka K., Schober F., 2004. Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*). *Am. J. Physiol.* 286(1): R174–R181.
- Aschwanden A., Beck M., Häberli C., Haller G., Kiene M., Roesch A., Sie R., Stutz M., 1996. Klimatologie der Schweiz, Klimatologie 1961–1990. Schweizerische Meteorologische Anstalt, Zurich. [in German]
- Bouche M., 1989. Le lièvre variable dans le massif des Écrins. Documents scientifiques du Parc National des Écrins. [in French]
- Burnham K.P., Anderson D.R., 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York.
- Chapus J.L., 1990. Comparison of the diets of two sympatric lagomorphs, *Lepus europaeus* (Pallas) and *Oryctolagus cuniculus* (L.) in an agroecosystem of the Ile-de-France. *Z. Säugetierkunde* 55: 176–185.
- Dahl F., 2005. Distinct seasonal habitat selection by annually sedentary mountain hares (*Lepus timidus*) in the boreal forest of Sweden. *Eur. J. Wildl. Res.* 51: 163–169.
- Gamboni A.-S., 1997. Comportement spatio-temporel d'une population de lièvre variable (*Lepus timidus varronis*) au sud des alpes. Diploma thesis, Institut of Zoology, University of Neuchâtel, Neuchâtel. [in French]
- Grace J., Easterbee N., 1979. Natural shelter for red deer (*Cervus elaphus*) in a Scottish glen. *J. Appl. Ecol.* 16(1): 37–48.
- Hewson R., Hinge M.D.C., 1990. Characteristics of the home range of mountain hares *Lepus timidus*. *J. Appl. Ecol.* 27(2): 651–666.
- Hick D.S., 1995. Does risk of predation influence population dynamics? Evidence from cyclic decline of snowshoe hares. *Wildl. Res.* 22: 115–129.
- Hiltunen M., 2003. Feeding intensity of mountain hares (*Lepus timidus*) during winter in Finland. *Mamm. Biol.* 68: 48–52.
- Hiltunen M., Kauhala K., 2006. Selection of sapling stand habitats by the mountain hare (*Lepus timidus*) during winter. *Mamm. Biol.* 71(3): 183–189.
- Hiltunen M., Kauhala K., Linden H., 2004. Habitat use of the mountain hare *Lepus timidus* in summer: the importance of different vegetation layers. *Acta Theriol.* 49(4): 479–490.
- Hirakawa H., 2001. Coprophagy in leporids and other mammalian herbivores. *Mammal Rev.* 31(1): 61–80.
- Hjalten J., Danell K., Ericson L., 2004. Hare and vole browsing preferences during winter. *Acta Theriol.* 49(1): 53–62.
- Hodges K.E., Sinclair A.R.E., 2003. Does predation risk cause snowshoe hares to modify their diets? *Can. J. Zool.* 81: 1973–1985.
- Hodges K.E., Mills L.S., 2008. Designing fecal pellet surveys for snowshoe hares. *For. Ecol. Manage.* 256(11): 1918–1926.
- Hollander M., Wolfe D.A., 1999. Nonparametric Statistical Methods. John Wiley & Sons, New York.
- Homolka M., 1982. The food of *Lepus europaeus* in a meadow and woodland complex. *Fol. Zool.* 31: 243–254.
- Homolka M., 1987. Problems associated with investigations into the diet of the European hare. *Fol. Zool.* 36: 193–192.
- Hulbert I.A.R., Iason G.R., Mayes R.W., 2001. The flexibility of an intermediate feeder: dietary selection by mountain hares measured using faecal n-alkanes. *Oecologia* 129(2): 197–205.
- Hulbert I.A.R., Iason G.R., Racey P.A., 1996. Habitat utilization in a stratified upland landscape by two lagomorphs with different feeding strategies. *J. Appl. Ecol.* 33(2): 315–324.
- Iason G.R., Van Wieren S.E., 1999. Digestive and ingestive adaptations of mammalian herbivores to low-quality forage. In: Olff H., Brown V.K., Drent R.H. (Eds.) *Herbivores: between plants and predators*. Blackwell Scientific, Oxford. 337–369.
- Jacobs J., 1974. Quantitative measurement of food selection – modification of forage ratio and Ivlev's Electivity Index. *Oecologia* 14(4): 413–417.
- Johannessen V., Samset E., 1994. Summer diet of the mountain hare (*Lepus timidus* L.) in a low-alpine area in southern Norway. *Can. J. Zool.* 72: 652–657.
- Johnson J.B., Omland K.S., 2004. Model selection in ecology and evolution. *Trends Ecol. Evol.* 19(2): 101–108.
- Katona K., Altbäcker V., 2002. Diet estimation by faeces analysis: sampling optimisation for the European hare. *Fol. Zool.* 51: 11–15.
- Krebs C.J., Boonstra R., Nams V., O'Donoghue M., Hodges K.E., Boutin S., 2001. Estimating snowshoe hare population density from pellet plots: a further evaluation. *Can. J. Zool.* 79(1): 1–4.
- Lindlöf B., Lindström E., Pehrson A., 1974. On the activity, habitat selection and diet of the mountain hare (*Lepus timidus*) in winter. *Viltrevy* 9: 27–42.
- Litvaitis J.A., Sherburne J.A., Bissonette J.A., 1985. A comparison of methods used to examine snowshoe hare habitat use. *J. Wildl. Manage.* 49(3): 693–695.
- Loidl B., 1997. Nahrungsökologie des Alpenschneehasen (*Lepus timidus varronis* Miller 1901) und Entwicklung einer molekularbiologischen Methode der Nahrungsanalyse von Herbivoren. PhD thesis, Faculty of Natural Sciences, Paris London University, Salzburg. [in German]
- Lotz A. (Ed.), 2006. Alpine Habitat Diversity – HABITALP – Project Report 2002–2006. Nationalpark Berchtesgaden, Berchtesgaden.
- Mole S., Rogler J.C., Morell C.J., Butler L.G., 1990. Herbivore Growth Reduction by Tannins: Use of Waldbauer Ratio Techniques and Manipulation of Salivary Protein Production to Elucidate Mechanisms of Action. *Biochem. Syst. Ecol.* 18: 183–197.
- Murray D., Ellsworth E., Zack A., 2005. Assessment of potential bias with snowshoe hare fecal pellet-plot counts. *J. Wildl. Manage.* 69(1): 385–395.
- Murray D.L., Roth J.D., Ellsworth E., Wirsing A.J., Steury T.D., 2002. Estimating low-density snowshoe hare populations using fecal pellet counts. *Can. J. Zool.* 80(4): 771–781.
- Nieminen P., Mustonen A.M., 2008. A preliminary study on the seasonal body temperature rhythms of the captive mountain hare (*Lepus timidus*). *Cryobiology* 56(2): 163–167.
- Nodari M., 2006. Ecological role of mountain hare (*Lepus timidus*) in the alpine ecosystem. Habitat use, population consistency and dynamics of a species of conservation and management interest. PhD thesis, Department of Environment, Health and Safety, University of Insubria, Unsubria.
- Paupério J., Alves P.C., 2008. Diet of the Iberian hare (*Lepus granatensis*) in a mountain ecosystem. *Eur. J. Wildl. Res.* 54: 571–579.
- Pehrson A., Lindlöf B., 1984. Impact of winter nutrition on reproduction in captive mountain hares (*Lepus timidus*). (Mammalia: Lagomorpha). *J. Zool. (London)* 204: 201–209.
- Putman R.J., 1984. Facts from faeces. *Mamm. Rev.* 14(2): 79–97.
- Pyörnilä A., Putaala A., Hissa R., Sulkava S., 1992. Adaptions to environment in the mountain hare (*Lepus timidus*) – thermal physiology and histochemical properties of locomotory muscles. *Can. J. Zool.* 70(7): 1325–1330.
- R Development Core Team, 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rao S.J., Iason G.R., Hulbert I.A.R., Racey P.A., 2003. The effect of establishing native woodland on habitat selection and ranging of moorland mountain hares (*Lepus timidus*), a flexible forager. *J. Zool.* 260: 1–9.
- Rehns M., Palme R., Filli F., Hackländer K., 2010. Seasonal glucocorticoid secretion in mountain hares (*Lepus timidus*). *Mammalia* 74(3): 347–350.
- Ruf T., Arnold W., 2000. Mechanisms of social thermoregulation in hibernating Alpine marmots (*Marmota marmota*). *Life in the Cold*: 81–94.
- Seccombe-Hett P., Turkington R., 2008. Summer diet selection of snowshoe hares: a test of nutritional hypotheses. *Oikos* 117: 1874–1884.
- Slotta-Bachmayr L., 1998. Biologie und Ökologie des Alpenschneehasen (*Lepus timidus varronis* Miller 1901). Verbreitung, Raumnutzung, Aktivität und Habitatwahl in den Hohen Tauern. PhD thesis, Faculty of Natural Sciences, Paris London University, Salzburg. [in German]
- Suter W., Suter U., Krusi B., Schutz M., 2004. Spatial variation of summer diet of red deer *Cervus elaphus* in the eastern Swiss Alps. *Wildl. Biol.* 10(1): 43–50.
- Tangney P., Fairley J., Odonnell G., 1995. Food of Irish hares *Lepus timidus hibernicus* in western Connemara, Ireland. *Acta Theriol.* 40: 403–413.
- Thulin C.-G., Flux J.E.C., 2003. *Lepus timidus* Linnaeus, 1758 – Schneehase. In: Krapp F. (Ed.) *Handbuch der Säugetiere Europas*, Band 3/II: Hasenartige Lagomorpha. Aula Verlag, Wiebelsheim. 155–185. [in German]
- Wolfe A., Whelan J., Hayden T.J., 1996. The diet of the mountain hare (*Lepus timidus hibernicus*) on coastal grassland. *J. Zool. Lond.* 240: 804–810.
- Wolff J.O., 1980. The role of habitat patchiness in the population dynamic of snowshoe hares. *Ecol. Monogr.* 50(1): 111–130.
- Zahler P., Khan M., 2003. Evidence for Dietary Specialization on Pine Needles by the Woolly Flying Squirrel (*Eupetaurus cinereus*). *J. Mamm.* 84: 480–486.
- Zweifel-Schielly B., Kreuzer M., Ewald K.C., Suter W., 2009. Habitat selection by an Alpine ungulate: the significance of forage characteristics varies with scale and season. *Ecography* 32:103–113.