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Diet selection by hares (*Lepus europaeus*) in arable land and its implications for habitat management

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Abstract Populations of European hares (*Lepus europaeus*) have experienced a dramatic decline throughout Europe in recent decades. European hares are assumed to prefer weeds over arable crops, and weed abundance was reduced by the intensification of agriculture. Therefore, modern agriculture has been blamed as a major factor affecting European hare populations. However, it is questionable whether European hares select weeds at all, as previous studies had major methodological limitations. By comparing availability and use of plants with Chesson's Electivity Index, we investigated whether the European hare actually feeds selectively on different plants in arable land. Food availability and use were dominated by cultivated crops (e.g. winter wheat, spring barley and sugar beet). Diet selection analysis revealed that in autumn and winter, European hares predominantly preferred cultivated crops (winter wheat) and food items provided by hunters (tubers of sugar beet and carrot). In spring and summer, apart from soy, only weeds (e.g. clover and corn poppy) were positively selected, especially after cereal crops were harvested. We suggest that the decline in European hare populations

throughout Europe was facilitated by the decrease in weed abundance. Wildlife-friendly set-asides in arable land have the potential to reconcile the European Union's Common Agricultural Policy with wildlife conservation.

Keywords Conservation · Set-aside · Weeds · Small game · Electivity

Introduction

The European hare (*Lepus europaeus* Pallas 1778) is widespread in Europe (Mitchell-Jones et al. 1999) and most common on intensively farmed arable land (Vaughan et al. 2003). However, hare populations have declined dramatically throughout Europe during recent decades (Flux and Angermann 1990; Mitchell-Jones et al. 1999). As a consequence, the European hare has been listed in Appendix III of the Berne Convention on the Conservation of European Wildlife and Natural Habitats (Anonymous 1979) and is classified as “near threatened” or even “threatened” on several Red Lists of Threatened Species, e.g. in Austria, Germany, Norway and Switzerland (Boye 1996).

Various factors may have contributed to the population decline, such as increased numbers of predators, climate change, diseases and human impact (e.g. agriculture, traffic, hunting) (Flux and Angermann 1990; Mitchell-Jones et al. 1999). Among these factors, the decrease in habitat quality due to the intensification of agriculture has been suggested as the most important (Edwards et al. 2000; Smith et al. 2005). This suggestion is consistent with the results of numerous dietary studies. Although European hares feed predominantly on cultivated crops, they seem to prefer weeds and wild grasses if these are available (Brüll 1973; Zörner 1977; Steineck 1978; Kammerer 1981; Homolka 1983; Frylestam 1986; Tapper and Barnes 1986; Späth 1989; Chapuis 1990; Hell et al. 2001). However, the intensification of agriculture has resulted in the reduced abundance of weeds on arable land (Jensen and Kjellsson 1995; Robinson and Sutherland 2002). It has been suggested that the reduction of weed abundance was a

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major factor causing the decline of European hare populations (Hackländer et al. 2002).

However, the link between the reduction of weed abundance on agricultural land and the decline of hare populations in Europe is weak, as there is no real evidence that the European hare feeds selectively on weeds. Most of the studies cited above failed to determine the use of different plants due to methodological limitations. In general, there are two methods to investigate food use in hares: (1) examination of post-ingestion samples, where the remains of food in the stomach or faeces are identified (stomach contents and faeces are examined microscopically; plant structures such as epidermis, cells and trichomes are used to determine plant species), and (2) observations of animals ingesting food (Litvaitis et al. 1996). The methodological limitations in previous studies on food use in European hares were that (1) the percentage of the different plant species in the stomach was estimated by analysing them only macroscopically (e.g. Zörner 1977), or (2) plant parts of the stomach contents were only put in rough categories (e.g. “green fodder” for any green plant parts) and not determined to the species level (e.g. Brüll 1973; Zörner 1977).

Moreover, a prerequisite for studies on food selection is to determine not only the use of a plant species but also its availability (see Krebs 1989). In addition, a selectivity index should be used, which not only takes into account the availability and use of a certain food type but also incorporates the number and the relative selection of other food types (Chesson 1983). Although some authors tried to include this, their results have to be interpreted with caution as (1) selection was shown not by using a computed index but by a visual comparison between availability and use percentages of plants in graphical plots (Kammerer 1981), (2) the availability was not determined from botanical inventories but from crop maps (Homolka 1983; Tapper and Barnes 1986; Späth 1989), or (3) the selection or preference indices used had a reduced expressiveness (Homolka 1983; Tapper and Barnes 1986).

Taken together, although many assumptions and conclusions exist in the literature about the European hare being a selective feeder preferring weeds over arable crops, this has not yet been shown empirically and on a quantitative basis. In this study, we investigated if European hares really feed selectively on different plants. The results are discussed in the context of reconciling modern agriculture with European hare conservation.

Materials and methods

The study was conducted in 2003 in four hunting grounds (total size 2,820 ha) in Lower Austria, approximately 40 km east of Vienna in the “Marchfeld” area ($48^{\circ}11'N$, $16^{\circ}42'E$, elevation 140 m above sea level). The area is dominated by intensively used arable land. Main crops are winter wheat (*Triticum aestivum*), sugar beet (*Beta vulgaris*), sunflower (*Helianthus annuus*), maize (*Zea mays*) and potato (*Solanum tuberosum*). Set-asides and fallow land represent approximately 7.5% of the study area. The availability of

food was analysed by botanical inventories, whereas the use of plants was determined by stomach content analysis.

Data collection

Food availability

We conducted botanical inventories in two consecutive weeks, each in February, May, August and November, using land registry maps of Austria (scale 1:25,000, Federal Office of Metrology and Surveying, Vienna, Austria). On the maps, we numbered each field (crop and set-aside). As woods, hedges, ditches and roads comprised less than 5% of the total area and these habitats are not a substantial part of arable land, they were not considered. The botanical inventory was done by estimating percent coverage of non-vital and vital parts of each plant species as well as bare soil on the total field. Plant nomenclature followed Lauber and Wagner (1998). Less common plants (less than 1% coverage) were listed as existing (modified after Braun-Blanquet 1964). The sum of vital parts of all plant species comprised the total food availability, as European hares rarely feed on non-vital plant parts (review in Zörner 1996 and Averianov et al. 2003).

Food use

For stomach collection, hares were shot with a rifle from a car ($n=110$) or collected as fresh road kills ($n=7$) in February ($N=37$), May ($N=28$), August ($N=32$) and November ($N=20$), in parallel to the vegetation inventory periods. To avoid any mixture of diet with reingested soft faeces due to caecotrophy (Hirakawa 2001), the sampling took place in the early morning after sunrise until approximately 10 a.m. The sample point of each hare was marked on the maps.

Stomach contents (excluding soft faeces) were weighed, thoroughly stirred, and at least 10 g was placed in a glass bowl (200 ml). Water of 10–20 ml was mixed with the sample. For botanical stomach content analysis, a method derived from Steineck (1978) and Klansek et al. (1995) was used. Small amounts of the mixture were put on a Petri dish with three equally sized chambers. Water was added into each of the three compartments so that the plant parts separated and floated. The samples in the Petri dish were then examined microscopically (at $1.25\times 4–10$ magnification), and plant parts were compared with a reference collection of plant samples for determination. The percentage of distinctive plant fragments, if possibly determined to the species level, was estimated. Plant fractions that accounted for less than 1% of items were marked as existing. Non-distinguishable fractions were noted as indefinable.

One Petri dish per stomach content was examined; the average percentage for each component of the stomach was calculated over the three compartments and used for further computations.

Determination of selectivity

We determined diet selection by using the Electivity Index “ ε ” presented by Chesson (1983; see Eq. (1)). This index is applied in diet selection studies (e.g. McKnight and Hepp 1998; Markkola et al. 2003), as it allows not only for the consideration of the availability (i.e. percentage of a particular plant species) of plants but also for the different numbers of available plants. This entails an advantage over other selection indices, e.g. Forage Ratio (Savage 1931) or Jacobs’ Selection Index D (Jacobs 1974), by weighting the preference of one plant relative to the average preference for the alternative plant species (Chesson 1983). The Electivity Index ε is based on Manly’s alpha Selection Index (α) (Manly et al. 1972; Eq. (2)). The conversion of Manly’s α to Chesson’s ε is done to obtain results that are comparable between cases for which the numbers of available plant species vary. This index can be used when the exploitation of plant species is a negligible factor (Krebs 1989), as was assumed to be the case in our survey. Additionally, Chesson’s Electivity Index ε incorporates all three criteria of suitability for an index of preference (Cock 1978): scale of index (negative and positive values are symmetrically distributed around zero), adaptability of index (more than two food types can be included) and range of index (maximum index values are attainable at all combinations of food densities). The index ε ranges between -1 and $+1$, with values between -1 and 0 showing a negative selection, whereas ε values between 0 and $+1$ indicate positive selection.

Eq. (1): Electivity Index ε (Chesson 1983). m = number of potential dietary types, α_i = Manly’s Selection Index for plant species i .

$$\varepsilon_i = \frac{m\alpha_i - 1}{(m - 2)\alpha_i + 1} \quad (1)$$

Eq. (2): Manly’s alpha Selection Index (α) (Chesson 1983). α_i = Manly’s Selection Index for plant species i ; r_i , r_j = proportions of plant species i and j in the diet (i and $j = 1, 2, 3, \dots, m$); n_i , n_j = proportions of plant species i and j available; m = number of potential plant species.

$$\alpha_i = \frac{r_i}{n_i} \frac{1}{\sum_{j=1}^m (r_j/n_j)} \quad (2)$$

To calculate the proportions of different food types in the environment, the area in which a hare may possibly have foraged (= r ; see Manly’s alpha Index, Formula 2) has to be defined. The most parsimonious approach is to calculate a maximal potential forage area (MPFA). According to the study of Reitz and Léonard (1994), who investigated the

habitat use of European hares in intensive arable land by telemetry, the mean distance between night (active) and day (inactive) location of a hare is 400 m. Since we did not know from which direction the hare came from prior to being sampled, we assumed that a hare’s MPFA is a circular area centred on the sample point with a radius of 400 m (approximately 50 ha). A circle drawn to scale, equivalent of a 50-ha area, with a grid of 81 grid nodes, was superimposed on the maps of the study sites, the centre of the circle being on the spot where the hare was collected. Taking the information from the botanical inventory, the botanical plant composition on each grid node was known (see “Food availability”). On the basis of the sum of those 81 points, average plant coverage on a hare’s MPFA was calculated. Indices ε were calculated for each individual hare (according to Eq. (1)). The indices for a certain plant taxon were then averaged over sampling periods. Preconditions for calculating the Electivity Index are values greater than zero for both the availability and the use of plant species. Some food items did not show up in the botanical inventory but were found in the hare’s stomach. To fulfil the preconditions for calculating ε , they were ascribed a coverage percentage of 0.01%. Animals that were collected too close to the border of the study area, i.e. which had at least 21 grid nodes outside the study area, were excluded from the analyses because food availability could not be determined with certainty.

Electivity Indices were calculated using MATLAB 6.5 (MathWorks Inc.). Due to the partly small numbers of hares, which positively selected for a particular plant, and due to the great variety in foraged plants among individuals, it was not possible to test for a significant difference to neutral selection using the bootstrap method.

Results

Food availability

The botanical inventory of the MPFAs showed that in February, hares had most access to wild mustard (*Sinapis arvensis*; 28%), mixed fields with wild mustard and lacy scorpion-weed (*Phacelia tanacetifolia*; 15%), as well as wood small-reed (*Calamagrostis epigejos*; 12%). In May, seedlings of winter wheat (*T. aestivum*; 52%) and spring barley (*Hordeum vulgare*; 22%) were the most available plants. In August, cereals had been harvested, and hares had the highest access to sugar beet (*B. vulgaris*; 27%) and maize (*Z. mays*; 13%). In November, the most available plants were lacy scorpion-weed (20%), wild mustard (18%) and small seedlings of winter wheat (13%; for a complete list of available plant species, see Appendix 1). During November and February, hunters provided food (carrots and sugar beets) to the hares. Those root crops were to be found scattered in the study sites in clusters. Their coverage percentage could not be estimated. Thus, they were not included in the list of the botanical inventory.

Table 1 Positively selected plant species

Period	Scientific name	ε	N	se
February	<i>Malus domestica</i>	0.96	1	–
	<i>Daucus carota</i>	0.87	3	0.08
	<i>Beta vulgaris</i>	0.83	22	0.08
May	<i>Trifolium repens</i>	0.87	2	0.07
	<i>Glycine max</i>	0.61	8	0.25
	<i>Trifolium pratense</i>	0.39	4	0.35
	<i>Papaver rhoes</i>	0.09	9	0.32
August	<i>Panicum miliaceum</i>	1.00	1	–
	<i>Papaver rhoes</i>	0.93	1	–
	<i>Trifolium incarnatus/suaveolens</i>	0.27	2	0.68
November	<i>Beta vulgaris</i>	0.98	5	0.02
	<i>Capsella bursa-pastoris</i>	0.85	1	–
	<i>Triticum aestivum</i>	0.19	20	0.21

ε mean Electivity Index, N number of hares that used the plant,
se standard error of the mean

Food use and selectivity

Of the 164 plant species available to hares (Appendix 1), we found a total of 49 in the hares' stomach contents ($N=117$; see Appendix 2). The mean percentage of unidentifiable material (stomach content material, which was heavily macerated and thus no recognizable structures apparent, or plant fragments not attributable to any species, or soil and dirt residues) was 0.13%. On average, a hare's stomach content consisted, in February ($N=37$), of 57% winter wheat sprouts (*T. aestivum*), 24% sugar beet tubers (*B. vulgaris*) and about 10% alfalfa (*Medicago sativa*); in May ($N=28$), again 50% winter wheat, 13% spring barley (*H. vulgare*) and 11% soy (*Glycine max*). In August, stomach contents ($N=32$) of hares consisted on average of about 39% alfalfa, 25% spring barley and 14% sugar beet tubers, and in November ($N=20$), of approximately 52% winter wheat, 22% sugar beet tubers and 17% alfalfa, respectively (Appendix 2). As mentioned before, sugar beet proportions in the stomach in November and February are root tubers that were provided by hunters. The high proportion of spring barley in August stems from out-growth (grains from the harvest). Hares showed positive Electivity Indices for only 11 out of the 49 used plants, i.e. 93% of all plants available were negatively selected and/or even not used (see Table 1).

Discussion

The aim of this study was to investigate whether European hares in intensive arable land selectively feed on weeds and grasses and avoid eating crops. We found that European hares most frequently used arable crops during the year. However, they did select weeds in spring and summer and preferred arable crops and food items provided by hunters in autumn and winter.

Looking at the different seasons in our study, we found that stomach contents in November contained little more

than 5% weeds and wild grasses; the remaining plants were all cultivated crops. During this time, freshly grown winter wheat was foraged by all sampled hares (mean percentage in all stomach contents greater than 51%), which resulted in a positive Electivity Index for this crop. Yet the standard error of the mean ε index is rather high due to the fact that the Electivity Indices for winter wheat varied greatly between the sampled hares, ranging from positive (ε index=1) to avoidance (ε index≈−1). Apart from that, sugar beet (tubers provided by hunters) was positively selected. In February, sprouts of winter wheat, sugar beet tubers and alfalfa accounted for more than 91% of the hares' stomach content, although these three plant species contributed only about 7% to the total food availability. However, winter wheat and alfalfa were not positively selected by hares because their availability was high compared to tubers of sugar beet and carrots, which were provided by hunters in small heaps. Consequently, these two food items were positively selected, and it is evident that two thirds of the sampled hares searched actively for this additional food. Similarly, over 83% of used plants in May were cultivated crops, which corresponded to their availability (more than 87%). However, we found that only the uncommon soy and rare weeds were positively selected by hares.

During August, hares positively selected three wild plant species, yet this result has only little explanatory power due to the very small sample size. The low number of positively selecting hares cannot be explained by the large number of available plant species ($n=108$) in August, as 60% of the sampled hares in May positively selected at least one of the four plant species listed in Table 1 when they had access to 105 different plant species. However, the proportion of plant species changed dramatically in summer. In May, more than 75% of food availability consisted of cereals. After the harvest in August, hares found vital plant parts mainly on crops of sugar beet, maize and sunflower (about 50% of food availability). On the other hand, approximately 21% of the available vital plants in August were weeds and wild grasses, resulting in comparably high proportions of these plants in the stomach contents (12%). As Chesson's Electivity Index considers both the availability of plant taxa and their abundance, it could be that due to the relative large number of wild grasses and weeds available, a positive selection for any plant species is quite unlikely.

Conclusions for habitat management

Arable land changed dramatically, and this change has been blamed to be the ultimate cause for the decline of European hares throughout Europe (Smith et al. 2005). In line with this, several studies have indicated that the positive effects of farming for European hares decreased as field size increased and habitat diversity decreased (Schröpfer and Nyenhuis 1982; Tapper and Barnes 1986; Lewandowski and Nowakowski 1993; Panek and Kamieniarz 1999; Vaughan et al. 2003; Jennings et al. 2006). Habitat diver-

sity is obviously a crucial factor especially in summer when—after cereals have been harvested—hares shift their food use towards other crops, selected weeds and fabaceae (this study). However, if the landscape is monotonous and consists of large fields of monocultures, one could predict that the ability of European hares to adapt their behaviour after harvesting (Marboutin and Aebischer 1996) is restricted: The alternative feeding sites for hares in summer might be far away and could act as hot spots for numerous other hares facing the same fate, resulting in potential risks of social stress (Lindlöf 1978; Monaghan and Metcalfe 1985), disease transmission and malnutrition (Tapper and Barnes 1986; Onderscheka 1996). Consistent with this, Frylestam (1980) showed that hares living in areas of low landscape diversity had lower body weights and survival rates than hares living in more diverse landscapes. Agricultural intensification resulted in lower landscape diversity and weed abundance (Jensen and Kjellsson 1995; Robinson and Sutherland 2002). As hares do selectively feed on weeds, if available, our study supports the hypothesis by Hackländer et al. (2002) that one proximate factor for the decline of European hare populations is a reduced availability of weed abundance.

Taking this line of evidence into account, protection strategies by wildlife conservationists should support weed abundance in arable land. This goal can be achieved in two ways: First, it has been shown that organic farming increases weed abundance (Hald 1999; Rydberg and Milberg 2000), at the same time, it increases the risk for European hares of being killed during mechanical weeding (Kelemen 2003). Second, weed abundance in arable land can be increased by the promotion of set-asides, as promoted by European societies for wildlife conservation (Anonymous 2000, 2003). Both might help to prevent a further decline of European hare populations in Europe and thus can reconcile Common Agricultural Policy (CAP) with the Berne Convention, which commits the European Union to ‘take appropriate and necessary legislative and administrative measures to ensure the protection of the wild fauna species specified in Appendix III’ (Anonymous 1979), in which the European hare is listed.

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Appendix 1

Plant taxa available to the sampled hares. The availability reflects the percentage of the sum of plant cover percentages for each individual taxon according to season in the MPFA of the 117 sampled hares; + indicates that this taxon was present, yet <0.1%.

Period	Scientific name	Percent
February	<i>Sinapis arvensis</i>	28.03
	<i>Sinapis arvensis/Phacelia tanacetifolia</i>	14.55
	<i>Calamagrostis epigejos</i>	11.51
	<i>Triticum aestivum</i>	5.38
	<i>Fabaceae</i>	4.22
	<i>Avenella flexuosa</i>	4.22
	<i>Pisum sativum/Phacelia tanacetifolia</i>	
	<i>Sinapis arvensis</i>	3.73
	<i>Pisum sativum</i>	3.22
	<i>Asparagus officinalis</i>	2.88
	<i>Arrhenatherum elatius</i>	2.54
	<i>Hordeum vulgare</i>	1.91
	<i>Medicago sativa</i>	1.87
	<i>Phragmites australis</i>	1.70
	<i>Stellaria media</i>	1.60
	<i>Bromus sterilis</i>	1.48
	<i>Zea mays</i>	1.17
	<i>Arrhenatherum elatius/Calamagrostis epigejos</i>	1.08
	<i>Poa pratensis</i>	1.04
	<i>Bromus japonicus</i>	<1
	<i>Bromus sp.</i>	<1
	<i>Cirsium arvense</i>	<1
	<i>Dactylis glomerata</i>	<1
	<i>Erigeron annuus</i>	<1
	<i>Fragaria vesca</i>	<1
	<i>Gramina sp.</i>	<1
	<i>Helictotrichon pubescens</i>	<1
	<i>Juncus filiformis</i>	<1
	<i>Lolium perenne</i>	<1
	<i>Matricaria recutita</i>	<1
	<i>Muscus sp.</i>	<1
	<i>Pisum sativum/Sinapis arvensis</i>	<1
	<i>Panicum miliaceum</i>	<1
	<i>Secale cereale</i>	<1
	Seedlings	<1
	<i>Solidago canadensis</i>	<1
	<i>Solidago virgaurea</i>	<1
	<i>Sorghum sudanense</i>	<1
	<i>Agropyron repens</i>	+
	<i>Allium cepa</i>	+
	<i>Avena sativa</i>	+
	<i>Beta vulgaris</i>	+
	<i>Brassica oleracea</i>	+

Period	Scientific name	Percent	Period	Scientific name	Percent
May	<i>Bromus ramosus</i>	+		<i>Achillea millefolium</i>	+
	<i>Calamagrostis</i> sp.	+		<i>Agrostis spica-venti</i>	+
	<i>Carex acutiformis</i>	+		<i>Amaranthus retroflexus</i>	+
	<i>Carex otrubae</i>	+		<i>Anthriscus sylvestris</i>	+
	<i>Carex</i> sp.	+		<i>Arctium lappa</i>	+
	<i>Composita</i>	+		<i>Arctium tomentosum</i>	+
	<i>Cornus sanguinea</i>	+		<i>Artemisia vulgaris</i>	+
	<i>Cynodon dactylon</i>	+		<i>Atriplex patula</i>	+
	<i>Daucus carota</i>	+		<i>Brachypodium pinnatum</i>	+
	<i>Galium verum</i>	+		<i>Bromus hordeaceus</i>	+
	<i>Holcus mollis</i>	+		<i>Bromus ramosus</i>	+
	<i>Juncus</i> sp.	+		<i>Capsella bursa-pastoris</i>	+
	<i>Lamium purpureum</i>	+		<i>Cardaria draba</i>	+
	<i>Lythrum salicaria</i>	+		<i>Carduus acanthoides</i>	+
	<i>Malus domestica</i>	+		<i>Carex acutiformis</i>	+
	<i>Mentha</i> sp.	+		<i>Chenopodium alba</i>	+
	<i>Papaver rhoeas</i>	+		<i>Conium maculatum</i>	+
	<i>Poaceae</i> sp.	+		<i>Consolida regalis</i>	+
	<i>Rumex obtusifolius</i>	+		<i>Convolvulus arvensis</i>	+
	<i>Syringa vulgaris</i>	+		<i>Conyza canadensis</i>	+
	<i>Urtica dioica</i>	+		<i>Cornus sanguinea</i>	+
	<i>Triticum aestivum</i>	52.39		<i>Cynodon dactylon</i>	+
	<i>Hordeum vulgare</i>	21.84		<i>Descurainia sophia</i>	+
	<i>Beta vulgaris</i>	5.85		<i>Dipsacus fullonum</i>	+
	<i>Pisum sativum</i>	1.95		<i>Epilobium roseum</i>	+
	<i>Secale cereale</i>	1.92		<i>Euonymus europaea</i>	+
	<i>Medicago sativa</i>	1.63		<i>Festuca ovina</i>	+
	<i>Helianthus annuus</i>	1.61		<i>Festuca rubra</i>	+
	<i>Calamagrostis epigejos</i>	1.44		<i>Galium aparine</i>	+
	<i>Zea mays</i>	1.24		<i>Galium mollugo</i>	+
	<i>Phaseolus vulgaris</i>	1.03		<i>Glycine max</i>	+
	<i>Agropyron repens</i>	<1		<i>Hordeum murinum</i>	+
	<i>Allium cepa</i>	<1		<i>Hypochaeris radicata</i>	+
	<i>Arrhenatherum elatius</i>	<1		<i>Lamium amplexicaule</i>	+
	<i>Asparagus officinalis</i>	<1		<i>Leontodon autumnalis</i>	+
	<i>Avena fatua</i>	<1		<i>Linaria vulgaris</i>	+
	<i>Avena sativa</i>	<1		<i>Lolium</i> sp.	+
	<i>Avenella flexuosa</i>	<1		<i>Lotus corniculatus</i>	+
	<i>Bromus japonicus</i>	<1		<i>Medicago sativa/Trifolium incarnatum</i>	+
	<i>Bromus sterilis</i>	<1		<i>Matricaria recutita</i>	+
	<i>Cirsium arvense</i>	1		<i>Medicago lupulina</i>	+
	<i>Dactylis glomerata</i>	<1		<i>Orchis</i> sp.	+
	<i>Daucus carota</i>	<1		<i>Panicum miliaceum</i>	+
	<i>Fabaceae</i>	<1		<i>Papaver rhoeas</i>	+
	<i>Fragaria vesca</i>	<1		<i>Poa annua</i>	+
	<i>Gramina</i> sp.	<1		<i>Poaceae and Fabaceae</i>	+
	<i>Lathyrus sativus</i>	<1		<i>Polygonum aviculare</i>	+
	<i>Lolium perenne</i>	<1		<i>Rubus caesius</i>	+
	<i>Phacelia tanacetifolia</i>	<1		<i>Rumex obtusifolius</i>	+
	<i>Phragmites australis</i>	<1		<i>Salvia sylvestris</i>	+
	<i>Poa pratensis</i>	<1		Shrubs	+
	<i>Sinapis arvensis</i>	<1		<i>Silene vulgaris</i>	+
	<i>Solidago canadensis</i>	<1		<i>Solanum dulcamara</i>	+
	<i>Solidago virgaurea</i>	<1		<i>Solanum tuberosum</i>	+
	<i>Urtica dioica</i>	<1		<i>Sonchus oleraceus</i>	+

Period	Scientific name	Percent	Period	Scientific name	Percent
August	<i>Sonchus</i> sp.	+		<i>Trifolium repens</i>	<1
	<i>Spinacia oleracea</i>	+		<i>Trifolium saxatile</i>	<1
	<i>Stellaria media</i>	+		<i>Urtica dioica</i>	<1
	<i>Symphytum officinale</i>	+		<i>Acer negundo</i>	+
	<i>Syringa vulgaris</i>	+		<i>Achillea millefolium</i>	+
	<i>Taraxacum officinale</i>	+		<i>Amaranthus alba</i>	+
	<i>Trifolium alexandrinum</i>	+		<i>Arctium lappa</i>	+
	<i>Trifolium pratense</i>	+		<i>Artemisia vulgaris</i>	+
	<i>Trifolium repens</i>	+		<i>Brachypodium pinnatum</i>	+
	<i>Trifolium</i> sp.	+		<i>Bromus japonicus</i>	+
	<i>Trifolium suaveolens</i>	+		<i>Bromus ramosus</i>	+
	<i>Tripleurospermum inodorum</i>	+		<i>Bromus</i> sp.	+
	<i>Veronica persica</i>	+		<i>Calystegia sepium</i>	+
	<i>Vicia faba</i>	+		<i>Carduus acanthoides</i>	+
	<i>Vicia sativa</i>	+		<i>Carduus</i> sp.	+
	<i>Viola arvensis</i>	+		<i>Carex acutiformis</i>	+
	<i>Beta vulgaris</i>	27.27		<i>Carex otrubae</i>	+
	<i>Zea mays</i>	13.30		<i>Carex pilulifera</i>	+
	<i>Helianthus annuus</i>	9.23		<i>Carlina vulgaris</i>	+
	<i>Medicago sativa</i>	8.24		<i>Conium maculatum</i>	+
	<i>Solanum tuberosum</i>	6.34		<i>Cornus sanguinea</i>	+
	<i>Asparagus officinalis</i>	4.37		<i>Datura stramonium</i>	+
	<i>Glycine max</i>	3.40		<i>Deschampsia caespitosa</i>	+
	<i>Avenella flexuosa</i>	2.70		<i>Descurainia sophia</i>	+
	Turf	2.16		<i>Echium vulgare</i>	+
	<i>Calamagrostis epigejos</i>	1.98		<i>Epilobium roseum</i>	+
	<i>Phaseolus vulgaris</i>	1.92		<i>Erigeron</i> sp.	+
	<i>Cirsium arvense</i>	1.84		<i>Euonymus europaea</i>	+
	<i>Chenopodium alba</i>	1.73		<i>Fagopyrum esculentum</i>	+
	<i>Hordeum vulgare</i>	1.35		<i>Fallopia convolvulus</i>	+
	<i>Triticum aestivum</i>	1.22		<i>Festuca rubra</i>	+
	<i>Daucus carota</i>	1.20		<i>Fraxinus excelsior</i>	+
	<i>Fabaceae</i>	1.12		<i>Galium aparine</i>	+
	<i>Pisum sativum</i>	1.01		<i>Galium mollugo</i>	+
	<i>Agropyron repens</i>	<1		<i>Galium verum</i>	+
	<i>Agrostis spica-venti</i>	<1		<i>Helictotrichon pubescens</i>	+
	<i>Allium cepa</i>	<1		<i>Hypochaeris radicata</i>	+
	<i>Amaranthus retroflexus</i>	<1		<i>Inula conyzoides</i>	+
	<i>Arrhenatherum elatius</i>	<1		<i>Juncus filiformis</i>	+
	<i>Bromus sterilis</i>	<1		<i>Lathyrus sativus</i>	+
	<i>Convolvulus arvensis</i>	<1		<i>Linaria vulgaris</i>	+
	<i>Conyza Canadensis</i>	<1		<i>Lotus corniculatus</i>	+
	<i>Dactylis glomerata</i>	<1		<i>Matricaria recutita</i>	+
	<i>Dipsacus fullonum</i>	<1		<i>Mentha aquatica</i>	+
	<i>Erigeron annuus</i>	<1		<i>Panicum miliaceum</i>	+
	<i>Fragaria vesca</i>	<1		<i>Papaver rhoeas</i>	+
	<i>Lactuca serriola</i>	<1		<i>Pastinaca sativa</i>	+
	<i>Lolium perenne</i>	<1		<i>Phleum pratense</i>	+
	<i>Lolium</i> sp.	<1		<i>Poaceae</i> sp.	+
	<i>Phacelia tanacetifolia</i>	<1		<i>Polygonum aviculare</i>	+
	<i>Phragmites australis</i>	<1		<i>Rubus caesius</i>	+
	<i>Poa pratensis</i>	<1		<i>Rumex obtusifolius</i>	+
	<i>Solidago canadensis</i>	<1		<i>Secale cereale</i>	+
	<i>Solidago virgaurea</i>	<1		<i>Securigera varia</i>	+
	<i>Solidago virgaurea</i>	<1		<i>Senecio vulgaris</i>	+

Period	Scientific name	Percent	Period	Scientific name	Percent
	<i>Setaria verticillata</i>	+		<i>Arctium lappa</i>	+
	<i>Setaria viridis</i>	+		<i>Arctium tomentosum</i>	+
	<i>Solanum dulcamara</i>	+		<i>Beta vulgaris</i>	+
	<i>Sonchus oleraceus</i>	+		<i>Brachypodium pinnatum</i>	+
	<i>Spinacia oleracea</i>	+		<i>Bromus ramosus</i>	+
	<i>Sympyrum officinale</i>	+		<i>Capsella bursa-pastoris</i>	+
	<i>Trifolium incarnatum/suaveolens</i>	+			
	<i>Taraxacum officinale</i>	+			
	<i>Trifolium alexandrinum</i>	+			
	<i>Trifolium suaveolens</i>	+			
	<i>Tripleurospermum inodorum</i>	+			
	<i>Tussilago farfara</i>	+			
	<i>Vicia faba</i>	+			
	<i>Vicia sativa</i>	+			
November	<i>Phacelia tanacetifolia</i>	20.43			
	<i>Sinapis arvensis</i>	17.60			
	<i>Triticum aestivum</i>	13.23			
	<i>Avenella flexuosa</i>	6.96			
	<i>Calamagrostis epigejos</i>	6.87			
	<i>Medicago sativa</i>	5.79			
	<i>Cirsium arvense</i>	3.16			
	<i>Bromus sterilis</i>	2.96			
	<i>Trifolium pretense</i>	2.78			
	<i>Lathyrus sativus</i>	2.74			
	<i>Arrhenatherum elatius</i>	1.96			
	<i>Vicia sativa</i>	1.70			
	<i>Solidago virgaurea</i>	1.53			
	<i>Pisum sativum</i>	1.26			
	<i>Conyza canadensis</i>	1.19			
	<i>Lolium perenne</i>	1.02			
	Seedlings	1.02			
	<i>Acer negundo</i>	<1			
	<i>Agropyron repens</i>	<1			
	<i>Agrostis spica-venti</i>	<1			
	<i>Amaranthus retroflexus</i>	<1			
	<i>Artemisia vulgaris</i>	<1			
	<i>Atriplex patula</i>	<1			
	<i>Avena fatua</i>	<1	May	<i>Triticum aestivum</i>	50.12
	<i>Bromus japonicus</i>	<1		<i>Hordeum vulgare</i>	12.93
	<i>Bromus sp.</i>	<1		<i>Glycine max</i>	11.32
	<i>Dactylis glomerata</i>	<1		<i>Trifolium pratense</i>	7.71
	<i>Dipsacus fullonum</i>	<1		<i>Beta vulgaris</i>	5.44
	<i>Festuca rubra</i>	<1		<i>Papaver rhoeas</i>	3.42
	<i>Leontodon autumnalis</i>	<1		<i>Trifolium repens</i>	2.52
	<i>Lolium sp.</i>	<1		<i>Secale cereale</i>	1.83
	<i>Lotus corniculatus</i>	<1		<i>Taraxacum officinale</i>	1.7
	<i>Muscus sp.</i>	<1		<i>Medicago sativa</i>	0.95
	<i>Phragmites australis</i>	<1		<i>Dactylis glomerata</i>	0.78
	<i>Poa pratensis</i>	<1		<i>Pisum sativum</i>	0.58
	<i>Rubus caesius</i>	<1		<i>Rubus caesius</i>	0.25
	<i>Sambucus nigra</i>	<1		<i>Arrhenatherum elatius</i>	0.13
	<i>Trifolium repens</i>	<1		<i>Agropyron repens</i>	+
	<i>Tripleurospermum inodorum</i>	<1		<i>Bromus hordeaceus</i>	+
	<i>Zea mays</i>	<1		<i>Bromus japonicus</i>	+
	<i>Achillea millefolium</i>	+		<i>Bromus sterilis</i>	+
				<i>Capsella bursa-pastoris</i>	+

Appendix 2

List of plant taxa found in the hares' stomachs ($N=117$). Sample periods being February ($N=18$ plants), May ($N=25$ plants), August ($N=24$ plants) and November ($N=20$ plants). Percentages shown as proportions of the sum of each individual plant taxon per period; + indicates that this taxon was present, yet $<0.1\%$.

Season	Scientific name	Percent
February	<i>Triticum aestivum</i>	57.07
	<i>Beta vulgaris</i>	24.14
	<i>Medicago sativa</i>	9.87
	<i>Sinapis arvensis</i>	2.78
	<i>Malus domestica</i>	2.04
	<i>Daucus carota</i>	1.85
	<i>Stellaria media</i>	1.44
	<i>Zea mays</i>	0.32
	<i>Galium verum</i>	0.14
	<i>Lamium purpureum</i>	0.14
	<i>Juncus capitatus</i>	0.12
	<i>Avenella flexuosa</i>	+
	Bark	+
	<i>Cirsium sp.</i>	+
	<i>Cornus sanguinea</i>	+
	<i>Dactylis glomerata</i>	+
	<i>Juncus sp.</i>	+
	<i>Taraxacum officinale</i>	+
May	<i>Triticum aestivum</i>	50.12
	<i>Hordeum vulgare</i>	12.93
	<i>Glycine max</i>	11.32
	<i>Trifolium pratense</i>	7.71
	<i>Beta vulgaris</i>	5.44
	<i>Papaver rhoeas</i>	3.42
	<i>Trifolium repens</i>	2.52
	<i>Secale cereale</i>	1.83
	<i>Taraxacum officinale</i>	1.7
	<i>Medicago sativa</i>	0.95
	<i>Dactylis glomerata</i>	0.78
	<i>Pisum sativum</i>	0.58
	<i>Rubus caesius</i>	0.25
	<i>Arrhenatherum elatius</i>	0.13
	<i>Agropyron repens</i>	+
	<i>Bromus hordeaceus</i>	+
	<i>Bromus japonicus</i>	+
	<i>Bromus sterilis</i>	+
	<i>Capsella bursa-pastoris</i>	+

Season	Scientific name	Percent	References
August	<i>Cirsium arvense</i>	+	Anonymous (1979) Convention on the conservation of European wildlife and natural habitats. Council of Europe, Strasbourg
	<i>Convolvulus arvensis</i>	+	Anonymous (2000) Europe after setaside. International Council for Game and Wildlife Conservation, Paris
	<i>Poa annua</i>	+	Anonymous (2003) Die Zukunft der Flächenstilllegung im Rahmen der EU-Agrarpolitik. Deutsche Wildtier Stiftung, Hamburg
November	<i>Polygonum aviculare</i>	+	Averianov A, Niethammer J, Pegel M (2003) <i>Lepus europaeus</i> Pallas, 1778—Feldhase. In: Niethammer J, Krapp F (eds) Handbuch der Säugetiere Europas, vol 3/II. Aula, Wiebelsheim, pp 35–104
	<i>Stellaria media</i>	+	Boye P (1996) Ist der Feldhase in Deutschland gefährdet? Nat Landsch 71:167–174
	<i>Trifolium pretense</i>	+	Braun-Blanquet J (1964) Pflanzensoziologie—Grundzüge der Vegetationskunde. Springer, Berlin Heidelberg New York
	<i>Trifolium repens</i>	+	Brüll U (1973) Wildfutterpflanzengesellschaften und Futterwert der von Feldhasen (<i>Lepus europaeus</i> Pallas) genutzten Pflanzen. PhD thesis, University of Hamburg, Hamburg
	<i>Zea mays</i>	+	Chapius JL (1990) Comparison of the diets of two sympatric lagomorphs, <i>Lepus europaeus</i> and <i>Oryctolagus cuniculus</i> , in an agroecosystem of the Ile-de-France. Z Säugetierkd 55:176–185
	<i>Medicago sativa</i>	38.79	Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. Ecology 64:1297–1304
	<i>Hordeum vulgare</i>	25.49	Cock MJW (1978) The assessment of preference. J Anim Ecol 47:805–816
	<i>Beta vulgaris</i>	13.87	Edwards PJ, Fletcher MR, Berny P (2000) Review of the factors affecting the decline of the European brown hare, <i>Lepus europaeus</i> (Pallas 1778) and the use of wildlife incident data to evaluate the significance of paraquat. Agric Ecosyst Environ 79:95–103
	<i>Artemisia vulgaris</i>	4.34	Flux JEC, Angermann R (1990) The hares and jackrabbits. In: Chapman JA, Flux JEC (eds) Rabbits, hares and pikas. The World Conservation Union (IUCN), Gland, pp 61–94
	<i>Daucus carota</i>	2.98	Frylestam B (1980) Utilization of farmland habitats by European hares (<i>Lepus europaeus</i> Pallas) in Southern Sweden. Viltrevy 11:276–284
	<i>Triticum aestivum</i>	2.45	Frylestam B (1986) Agricultural land use effect on the winter diet of Brown hare (<i>Lepus europaeus</i> Pallas) in Southern Sweden. Mamm Rev 16:157–161
	<i>Taraxacum officinale</i>	2.31	Hackländer K, Tataruch F, Ruf T (2002) The effect of dietary fat content on lactation energetics in the European hare (<i>Lepus europaeus</i>). Physiol Biochem Zool 75:19–28
	<i>Zea mays</i>	2.3	Hald AB (1999) Weed vegetation (wild flora) of long established organic versus conventional cereal fields in Denmark. Ann Appl Biol 134:307–314
	<i>Avenella flexuosa</i>	1.77	Hell P, Slamečka J, Homolka M, Jurčík R, Poláčková M (2001) Einfluss intensiver großflächiger Landwirtschaft auf die Nahrungsökologie des Feldhasen im slowakischen Teil der Donauebene. Hung Small Game Bull 6:13–30
	<i>Glycine max</i>	1.44	Hirakawa H (2001) Coprophagy in leporids and other mammalian herbivores. Mamm Rev 31:61–80
	<i>Agropyron repens</i>	1.18	Homolka M (1983) The diet of <i>Lepus europaeus</i> in the agroecosystems. Acta Sci Nat Acad Sci Bohemoslov (Brno) 17:1–41
	<i>Amaranthus retroflexus</i>	1.03	Jacobs J (1974) Quantitative measurement of food selection: a modification of the Forage Ratio and Ivlev's Electivity Index. Oecologia 14:413–417
	<i>Panicum miliaceum</i>	0.88	Jennings NV, Smith RK, Hackländer K, Harris S, White PCL (2006) Variation in demography, condition, and dietary quality of hares <i>Lepus europaeus</i> from high-density and low-density populations. Wildl Biol (in press)
	<i>Dactylis glomerata</i>	0.64	Jensen HA, Kjellsson G (1995) Frøpuljens størrelse og dynamik i moderne landbrug 1. Ändringer af frøindholdet i agerjord 1964–1989. Miljostyr Bekæmpmiddelforsk Miljostyr 13:1–141
	<i>Polygonum aviculare</i>	0.12	Kammerer E (1981) Bestimmung der Quantität und Qualität der aufgenommenen Äsung und Rückschluss auf die Größe des Tagesaktivitätsraumes des Feldhasen— <i>Lepus europaeus</i> Pallas —im Waldviertel (Raum Schrems). PhD thesis, University of Veterinary Medicine, Vienna
	<i>Fagopyrum esculentum</i>	0.1	Kelemen J (2003) Biologischer Landbau und Artenschutz. G'stettin 54:3–5
	<i>Lathyrus sativus</i>	0.1	
	<i>Arrhenatherum elatius</i>	+	
	<i>Convolvulus arvensis</i>	+	
	<i>Hordeum murinum</i>	+	
	<i>Lotus corniculatus</i>	+	
	<i>Papaver rhoeas</i>	+	
	<i>Taraxacum officinale</i>	+	
	<i>Thymus serpyllum</i>	+	
	<i>Trifolium incarnatum/suaveolens</i>	+	
	<i>Triticum aestivum</i>	51.86	
	<i>Beta vulgaris</i>	21.72	
	<i>Medicago sativa</i>	17.37	
	<i>Sinapis arvensis</i>	3.65	
	<i>Arrhenatherum elatius</i>	1.65	
	<i>Avenella flexuosa</i>	1.6	
	<i>Trifolium pratense</i>	1.19	
	<i>Bromus</i> sp.	0.52	
	<i>Dactylis glomerata</i>	0.35	
	<i>Agropyron repens</i>	+	
	<i>Amaranthus retroflexus</i>	+	
	<i>Artemisia vulgaris</i>	+	
	<i>Capsella bursa-pastoris</i>	+	
	<i>Crataegus</i> sp.	+	
	<i>Helicotrichon pubescens</i>	+	
	<i>Malus domestica</i>	+	
	<i>Phacelia tanacetifolia</i>	+	
	<i>Plantago lanceolata</i>	+	
	<i>Stellaria media</i>	+	
	<i>Zea mays</i>	+	

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