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SPATIAL, TEMPORAL AND INDIVIDUAL VARIABILITY IN THE AUTUMN DIET OF EUROPEAN HARE (*LEPUS EUROPAEUS*) IN HUNGARY

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The number of European hares (*Lepus europaeus* PALLAS, 1778) has been on the decline for several decades, mainly due to the intensification of agriculture that has decreased variability in the hare's food supply. Therefore, our aim was to investigate the variability in the diet of hares in agricultural, pastural and woody habitat types. Microhistological analysis of stomach contents was used to define the plant species eaten by hares. Our results show that the European hare diet is greatly varied (24 species were eaten). The dominant cultivated species in the diet was wheat, *Triticum aestivum*. Grasses and browses were also important food components in every area. Among browses we found a generally high consumption of elderberry, *Sambucus* spp. Hares consumed forbs and seeds in smaller proportions. When possible, hares select a varied diet; even in faeces collected in different cultivations the given cultivated plant species was not dominant. Individual variability in diet composition was also high. Hare habitats should be improved by providing patchy habitat with various field edges, which are connected together (green corridor system). Elderberry should be grown in hedges, and wheat favoured in monocultures.

Key words: cultivated plants, elderberry, habitat heterogeneity

INTRODUCTION

The number of European hares (*Lepus europaeus* PALLAS, 1778) has drastically decreased in Hungary (KOVÁCS & HELTAY 1985, CSÁNYI 1996), as well as in the whole of Europe (MITCHELL-JONES *et al*. 1999, EDWARDS *et al*. 2000) since the 1960's. SMITH *et al*. (2005*a*) showed that the ultimate cause for the decline was the intensification of agriculture. European hares prefer heterogeneous habitats with variable food supply and sufficient shelter during the year (SMITH *et al*. 2004). The increase in the number of large monocultures has resulted in a disappearance of their preferred habitat. Although there have been several foreign studies on the population declines (SLAMEČKA *et al*. 1997, VAUGHAN *et al*. 2003) and food habits of European hares (HOMOLKA 1982, 1983, 1987*a*, CHAPUIS 1990, VAN DER WAL *et al*. 1998), at least in Hungary there has been no appreciation of the changing status of the species. The owners of several hunting units do not understand the need for conservation of European hares; for example, of the need to significantly improve their habitats (BIRÓ & SZEMETHY 2002).

The diet composition of European hares has already been described in numerous foreign studies (BRÜLL 1976, HEWSON 1977, HOMOLKA 1982, 1983, 1987*a, b*, CHAPUIS 1990, SLAMEČKA *et al*. 1997, HOMOLKA *et al*. 1999, REICHLIN *et al*. 2006), but there have only been some small focused studies in Hungary (DEMETER & MÁTRAI 1988, KATONA *et al*. 2004). FRYLESTAM (1986) found that European hares prefer wild (not cultivated) species (grasses, forbs) over cultivated ones, both in pastures and cultivated areas. Moreover, their diet is much more variable in pastures than in areas dominated by monocultural fields (37 *vs* 14 species).

Although we know that hare diet can be highly variable, some of the components of this variability are poorly discussed in the literature (*e.g.* individual variability: KATONA & ALTBÄCKER 2002). However, this information would be important to manage hare populations and their habitats not only in a general way (e.g. that field edges are necessary), but based on a more detailed knowledge (e.g. the required plant species in those field edges). The managers have to consider the spatial, temporal and individual alterations. Via our research we expected to obtain actual information on the dietary characteristics of the European hare in Hungary and describe the factors of their diet variability, such as differently managed habitats and cultivations, consecutive years and individual differences.

MATERIALS AND METHODS

Study area

Investigations were carried out in 5 different rural areas named after adjacent urban areas in the eastern part of Hungary between 2000 and 2002 (Fig. 1). At the Kompolt, Csongrád and Abádszalók sites a considerable part of the area was under agricultural cultivation (agricultural study sites). Expanded monocultures were the most typical in the first area. In Apaj pastures and fallow lands occupied half of the area (pastural study site). In Lakitelek woody patches dominated the habitat (woody study site). The proportion of different vegetation types (coverage % in the hunting unit area) and the field sizes in those study areas are shown in Table 1. The largest field sizes refer to the maximum size of homogenous arable blocks in the areas.

According to spotlight estimations undertaken in the autumn of 2002, the hare population density (individual/100 ha, mean±SD) was 25±5 in Kompolt, 50±14 in Csongrád, 70±17 in Abádszalók, 15±3 in Apaj and 42±6 in Lakitelek (BIRÓ & SZEMETHY 2002).

Microhistological diet composition analysis

Diet composition of European hares in different study areas was compared by means of microhistological analysis from stomach contents (KATONA & ALTBÄCKER 2002, KATONA *et al*. 2004). Earlier studies showed that the results on the diet composition of hares can be very similar by analysing stomach contents or faecal pellets (HOMOLKA 1986). Stomachs were collected from individuals shot during drive hunts in autumn (October–December). From Kompolt and Csongrád, we had samples in 3 consecutive years (2000–2002), from Apaj for 2 years (2000–2001), while from Abádszalók and Lakitelek only in 2002. Samples were stored deep-frozen (–18 °C) until the dietary studies were carried out. For details of sample sizes see Table 2.

Stomachs were opened with a bistoury and their contents put into Petri-dishes. Taking out randomly small pieces of content from each dish we made composite (mixed) samples representing all the hares shot in each area and each year. Then we took sub samples from the homogenised sample, and put it into a test-tube. We added 20% nitric acid to the sample and boiled it for 1.5 sec. Epidermal fragments were dispersed evenly in 1–2 drops of glycerine and one drop of 0.2% Toluidine-Blue on the slides. These samples were covered with cover slips and investigated under a microscope at 160× magnification. We made 3 slides for each area per year. On each of them 100 randomly selected epidermis fragments were identified to species or to the most accurate systematic category (MÁTRAI *et al.* 1986). Data of the 3 slides were averaged to determine the proportion of the plants species in the diet.

In 2002 the stomach contents of 20 young females originated from the whole Kompolt hunting area during the autumn hunt were examined to determine individual differences in dietary composition. For each individual (not mixed) sample 100 epidermal fragments were identified. These stomachs became the part of the yearly composite sample of the area, too.

In September of 2002, 50 fresh hare droppings were collected from 6 different agricultural cultivations (sunflower *Helianthus annuus*, sugar beet *Daucus carota*, lucerne *Medicago sativa*, maize *Zea mays*, stubble-field and plough) in Csongrád to investigate the extent to which hares exploited the resources of multiple fields. The size of the fields varied between 10 and 100 ha, which is similar to the

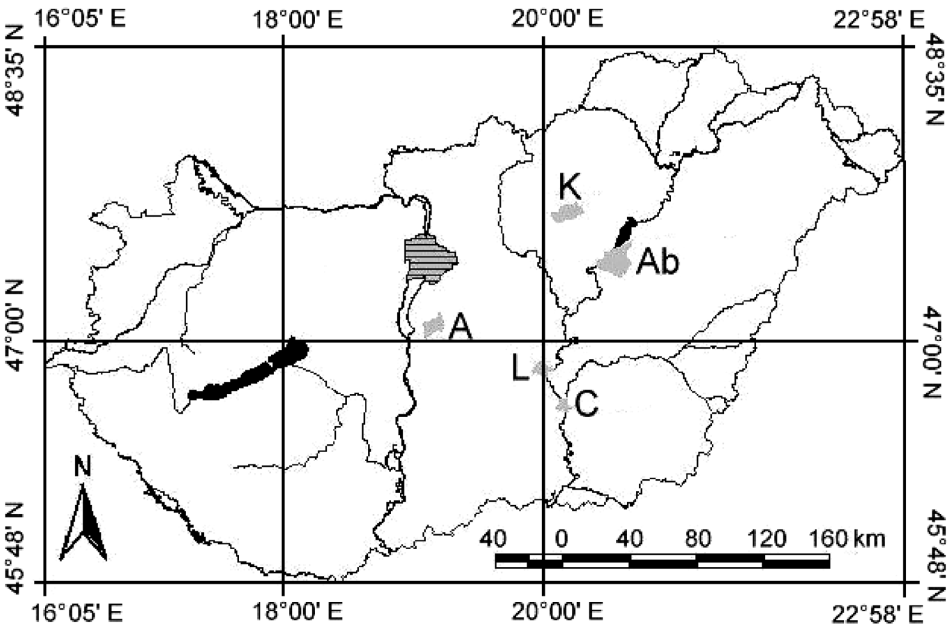

Fig. 1. Localities of the study areas. Study areas are shown as gray patches, the capital (Budapest) by striped gray area, Lake Balaton and Lake Tisza by black ones. Black lines are Hungarian rivers and the national border. A: Apaj, Ab: Abádszalók, C: Csongrád, K: Kompolt, L: Lakitelek

home range size of the European hare on the Central European Plain (35–100 ha) (HOMOLKA 1985, KOVÁCS & BÚZA 1988). The distances between different cultivations studied were between 0 and 1500 m, in most cases potentially coverable by hares.

The pellets were homogenized to a composite sample for each field and 100 epidermal fragments were identified from each sample. Those faecal pellets were not included into the yearly composite sample mixed from stomach contents of the area.

Table 1. Spatial characteristics of the study areas and distribution [coverage % in the hunting unit areas] of the vegetation types.

	Kompolt	Csongrád	Abádszalók	Apaj	Lakitelek
Locality	47°44'N, 20°15'E	46°43'N, 20°09'E	47°28'N, 20°36'E	47°07'N, 19°05'E	46°52'N, 20°00'E
Area size (ha)	11421	2689	18172	8113	5110
Field sizes (ha)	5-200	10-100	0.5 -60	1 - 50	1 - 50
Vegetation type	agricultural	agricultural	agricultural	pastural	woody
	Coverage of vegetation types in the hunting areas (%)				
Cultivated fields	71	46	54	26	23
Cereals	20	27	31	16	15
Maize	7		3	8	6
Lucerne				1	2
Rape	26		5		
Sunflower	18		13	1	
Row crops		12			
Forage plants		7			
Other			2		
Orchard	11	4	0	0	23
Apple					15
Vineyard		1			8
Melon	3				
Other	8	3			
Uncultivated areas	0	21	0	3	2
Grassland	4	13	7	65	0
Wetland	1	8	11	5	0
Lake		7	10	5	
Reed	1	1	1		
Forest	8	6	16	1	52
Settlement	0	0	2	0	0
Other	5	2	10	0	0

Statistical analysis

Changes in diet composition between years and areas and the proportion of consumed plant species in different cultivations and by different individuals were examined using a χ^2 homogeneity-test with Bonferroni-intervals as a post-hoc test (BYERS *et al.* 1984). Preference indices were not calculated, because we knew the proportion of different vegetation types only for the area, but not at the level of individual species.

We calculated the Shannon diversity index (KREBS 1989) for each area and year to characterize the diet composition of hares:

$$H' = -\sum p_i \times \ln p_i$$

where $p_i = \frac{n_i}{N}$, n_i = the number of epidermis fragments of the species i, N= total number of epidermis fragments in the sample (n = 100).

We also calculated the evenness of their diet using the Shannon diversity index (H') and the number of species (S) (KREBS 1989):

$$E = \frac{H'}{\ln S}$$

We compared the diet diversity between years and areas by a modified t-test (HUTCHESON 1970).

RESULTS

Variability in the diet composition

There were remarkable differences in the dietary composition of European hares between areas (in 2000: $\chi^2 = 82.5$, df = 26, $p < 0.001$, in 2001: $\chi^2 = 138.4$, df = 36, $p < 0.001$, in 2002: $\chi^2 = 339$, df = 45, $p < 0.001$). On the pastural study site monocotyledons (44%) and browses (32%) constituted the main part of the diet in 2000. However, in 2001 browses became dominant in the diet (61%). The monocotyledons (32%) and cultivated plants (36%) were dominant on the woody study site. In contrast, on arable land hares consumed cultivated plants in the greatest quantity (19–58%). However, even there, browses were the dominant food components in some years (7–45%). Among browses, elder was consumed in the greatest proportion (5–41%) in every area (Table 2).

There were great differences in the consumption of cultivated plants between years and areas ($\chi^2 = 135$, df = 9, $p < 0.001$). Hares ate relatively less of the cultivated plant species on the pastural study site (Apaj) than the average of all of the areas in 2000 and 2001. Similar results were found on the arable land at Kompolt in 2002, while in Csongrád (also arable land) hares ate remarkably more of the cultivated plants than the average in 2000 and 2002. Among the cultivated plants wheat was the dominant species in every area; beside this only lucerne was consumed in a noticeable quantity (Table 2).

Table 2. Diet composition [average of the three analyses in %; relative occurrence of the items of the components] of the European hare in the hunting areas during the study period. Agricultural study sites: Kompolt, Csongrád, Abádszalók. Pastural study site: Apaj. Woody study site: Lakitelek.

	Kompolt			Csongrád			Abád-szalók	Apaj		Laki-telek
Sample size	38	23	57	37	50	33	36	21	26	39
Year	2000	2001	2002	2000	2001	2002	2002	2000	2001	2002
Cultivated plants	45	49	19	55	42	58	37	15	12	36
Triticum aestivum	44	43	17	46	24	58	36	11	7	27
Triticum a. (seed)	0	5	2	9	7	0	0	3	0	0
Medicago sativa	1	0	0	0	11	0	1	1	2	9
Brassica napus	0	1	0	0	0	0	0	0	3	0
Grasses	11	20	14	18	10	8	45	44	15	32
Festuca spp.	7	6	6	5	5	4	26	14	5	16
Cynodon dactylon	0	1	0	0	1	1	0	3	0	0
Bromus spp.	0	0	1	0	0	0	10	0	0	8
Carex spp.	0	0	0	0	1	3	1	0	1	1
Agropyron repens	3	13	3	10	3	0	1	22	7	1
Secale sylvestre	0	0	0	0	0	0	0	5	0	0
Other grasses	1	0	4	3	0	0	7	0	2	6
Forbs	8	4	11	0	6	17	2	3	5	4
Chaenopodium spp.	0	0	9	0	0	6	1	0	0	1
Capsella bursa pastoris	1	0	0	0	0	0	0	0	3	0
Crepis spp.	2	3	1	0	1	1	1	0	1	2
Other forbs	5	1	1	0	5	10	0	3	1	1
Browses	29	23	45	26	36	17	7	32	61	18
Sambucus spp.	21	18	41	18	25	12	5	24	26	17
Pinus spp.	0	0	0	0	1	0	0	0	0	0
Gleditsia (seed)	0	0	0	0	2	0	0	0	0	0
Eleagnus angustifolia	0	0	0	0	2	0	1	0	25	0
Prunus spinosa	0	0	0	0	4	0	0	0	1	0
Rubus spp.	1	0	1	1	0	0	1	0	3	1
Unidentified barks	7	5	3	7	2	5	0	8	6	0
Other seeds	7	4	11	1	6	0	9	6	7	10
Species number	13	8	10	7	14	10	12	10	14	12
Diversity	1.55	1.38	1.58	1.21	1.93	1.39	1.67	1.79	2.02	1.94
Evenness	0.60	0.66	0.68	0.62	0.73	0.60	0.67	0.78	0.76	0.78

Table 3. Diet composition [%] of European hares determined from faeces collected in different cultivations in Csongrád (agricultural study site) in September 2002.

	Vegetation					
Diet	Sunflower	Sugar beet	Lucerne	Maize	Stubble	Plough land
Wheat	8	14	17	11	14	15
Lucerne	10	3	13	13	13	2
Maize	16	2	12	9	3	0
Sunflower	8	0	1	0	0	2
Sugar beet	1	2	0	2	0	2
Grasses	24	58	27	34	36	41
Forbs/browses	33	21	30	31	34	43

In faeces collected in different cultivations the given cultivated plant species was not dominant and more cultivated species were always recognized. The proportion of wheat was similar in the hare faeces from every cultivated field. However, the occurrence of the other plants in the faeces differed in the case of certain cultivations (lucerne: $\chi^2 = 17.7$, df = 5, $p < 0.01$; maize: $\chi^2 = 30$, df = 5, $p < 0.001$; other monocotyledons: $\chi^2 = 31.5$, df = 5, $p < 0.001$; other dicotyledons: $\chi^2 = 13.1$, df = 5, $p < 0.05$). The proportion of lucerne and maize was not significantly higher in the faecal pellets collected in lucerne- or maize-fields, respectively. The proportion of lucerne and maize was smaller than the average on sugar beet field and plough-land, while that of maize was higher on sunflower-fields (Table 3).

The individual variety of diet composition was high (Table 4; $\chi^2 = 713.64$, df = 76, $p < 0.001$). The diet composition of the individuals always differed from that of the composite (mixed) sample ($p < 0.05$).

Diet diversity

Our investigations showed that the autumn diet of European hares contained various plant species (24 species during 3 years). Diversity values were more variable, while the evenness values were more balanced.

Diet diversity was similar in Apaj and Kompolt between years, while in Csongrád the value was higher in 2001 (2000–2001: $t = 4.9$, df = 183.5, $p < 0.001$, 2001–2002: $t = -3.4$, df = 185.4, $p < 0.001$). However, there were significant differences between the areas in the same years. There were differences between Kompolt and Csongrád in 2000 and in 2001 (in 2000: $t = -2.1$, df = 165.9, $p < 0.05$, in 2001: $t = 3.8$, df = 181.9, $p < 0.001$), between Apaj and Csongrád in 2000 ($t = -4.5$, df = 171.1, $p < 0.001$), and between Apaj and Kompolt in 2001 ($t = -4.4$, df = 176.4, $p < 0.001$). In 2002 the arable lands did not differ from each other. In

Table 4. Diet composition [%] of the young female European hare individuals in Kompolt (agricultural study site) in 2002.

Individual code	Proportion in the diet (%)				
	Triticum aestivum	*Sambucus* spp.	Grasses	Forbs	Seeds
1	0	38	15	25	22
2	2	33	26	30	9
3	20	11	40	21	8
4	4	48	11	30	7
5	1	33	19	17	30
6	4	14	22	33	27
7	4	40	11	25	20
8	3	41	9	19	28
9	5	40	25	17	13
10	7	33	13	26	21
11	20	28	24	22	6
12	1	34	13	29	23
13	2	37	14	22	25
14	59	1	25	12	3
15	1	32	38	11	18
16	21	17	23	28	11
17	30	15	23	24	8
18	41	6	23	8	22
19	1	28	14	29	28
20	5	28	21	24	22
Composite sample	20	43	15	11	11

this year the diversity was the highest on the woody study site (Abádszalók–Lakitelek: $t = 2$, $df = 173.2$, $p < 0.05$; Kompolt–Lakitelek: $t = 2.7$, $df = 164$, $p < 0.01$; Csongrád–Lakitelek: $t = 3.8$, $df = 168.9$, $p < 0.001$) (Table 2).

DISCUSSION

Our results revealed that hares endeavoured to consume a diverse diet when they had access to many different plant species. We identified 24 plant species in the samples ($n = 350$) originating from 5 study areas. Among those components the role of wheat and that of the elder should be emphasised. Compared to this, the proportion of other species was remarkably lower; 50% of the diet was constituted by

1–3 plant species in most cases. This corresponds to HOMOLKA's observations (1983), according to which only a few plant species constituted the major part of the diet of hares at any particular point in time. It is clear generally that the food availability in any habitat influences the number of consumed species and diet diversity. FRYLESTAM (1986) found that the diet of hares was the most varied on pastural land, while it varied least on monocultural areas; moreover they always preferred wild plant species to cultivated ones (see also SMITH *et al*. 2005*b*). However, our results were more complex. Neither diet diversity nor the number of consumed species was always higher in pastural areas (Apaj), than on extended arable lands (*e.g*. Kompolt). However, the diet of hares was dominated by cultivated species on intensively cultivated agricultural areas (Kompolt, Csongrád), where only a smaller proportion of the diet was composed of wild plant species. But wild species were important food components not only on pastural land, but even at Abádszalók and Lakitelek, where grassy areas were scarce.

Our results confirmed that hares consumed more cultivated plant species in intensively cultivated agricultural areas than in areas with pastures and fallowlands (SMITH *et al*. 2005*b*). The dominance of wheat among cultivated plants eaten corresponds to foreign studies (FRYLESTAM 1986, CHAPUIS 1990). Although lucerne was also consumed in every area, it constituted a much lower part of the diet than did wheat. In the earlier Hungarian study (DEMETER & MÁTRAI 1988) the proportion of this plant was higher (19%), and it was also important (21%) in HOMOLKA's investigations (1983) in agrocenoses. But its proportion was very low in other foreign studies, 0.1% on pastures (FRYLESTAM 1986), and less than 2% in 6 different areas in the Czech Republic (HOMOLKA 1987*a*). In our studies the consumption of rape was very low (0–3%), and it occurred only one year in 2 areas. BRÜLL (1976) and FRYLESTAM (1986) found this plant represented a much higher proportion of the diet (15–39%). However, FRYLESTAM (1986) stated that hares avoid this plant in late autumn due to its content of glucosinulates. CHAPUIS (1990) also mentioned that a kind of rape (named "00") could have been responsible for the mortality of wild animal populations. Maize and sunflower had been harvested before hunting commenced, thus these plants could not occur in the diet of the shot hares.

In our study browses always played a significant role in the diet of hares, even in the areas with negligible forest cover. It shows that hares did not consume browse in the forest, but rather those in the margins of crop fields and forests. Many researchers have noted that the proportion of browse increases in the winter diet of hares (HOMOLKA 1982, 1983, 1987*a*, KATONA *et al*. 2004, RÖDEL *et al*. 2004). However, elderberry has never been revealed as an important food component of European hares in other studies (RÖDEL *et al*. 2004). In spite of this we found that hares consumed this plant in considerable amounts (mean±SD: 20.7±9.5, range: 5–41%) in each of our study areas. The general preference to this shrub in all study areas can be explained by the high protein content of this plant (up to 36%, SZEMETHY *et al*. 2003).

We identified high individual variability in the diet. These differences are not surprising as every individual uses different home ranges with more or less different food availability and has slightly different food preferences developed by individual learning process (ALTBÄCKER *et al*. 1995). It also illustrates that diet composition determined for the whole population from a composite sample could bias our suggestions for management. We have to consider that individual diets can significantly differ from the composite sample ("diet composition of the population"), which reveal principally the relative effect of the herbivore population as a whole on the different species of the vegetation (KATONA *et al*. 2004). Individual differences in the diet have also been observed in deer species (MÁTRAI & KABAI 1989, HOMOLKA & HEROLDOVÁ 1992).

In the everyday practice considering this individual variability is not easy for game managers. Detecting the increasing individual differences they can reveal the adaptability of this game species to the changing vegetation. In one hand it obligates managers to provide a "collection" selected from the preferred plant species in a diverse habitat throughout the year. On the other hand this diversity allows managers to select this supply considering their actual budget and market circumstances.

In conclusion we state that there is high spatial, temporal and individual variability in the diet composition of the European hare. Since hares use a small home range 35–100 ha on Central European Plain (HOMOLKA 1985, KOVÁCS & BÚZA 1988) they prefer to occupy those places, where different cultivations and pastures are easily accessible for a varied diet. Our results demonstrate that hares do not restrict themselves to the plant resources of a single cultivated field, but forage across several fields. That is why a heterogeneous agricultural habitat structure should be established, incorporating various kinds of plants in many smaller plots. Meadows, uncultivated patches occupied by grasses and legumes and the original wild vegetation of the field edges could provide diverse wild flora as food supply to hares. Elderberry growing along the edges can be also a preferred food for hares. Availability of winter wheat at least in smaller patches in the intensively cultivated arable lands can be favourable for hares in the autumn-winter period, as it can provide relatively good quality food in the absence of wild flora.

Although our results did not cover an entire year, they showed that there are several components causing high variability in the diet of hare. Therefore providing an evenly-scattered, diverse food supply in the area permanently throughout the year could help hares to survive and their populations to increase in Central Europe.

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