

Competition between European hare and European rabbit in a lowland area, Hungary: a long-term ecological study in the period of rabbit extinction

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Abstract. Abundance of the European hare (*Lepus europaeus* Pallas, 1778) has been declining dramatically in Europe. In the framework of our long-term ecological studies in the juniper forest at Bugac, Hungary, we have also monitored its population abundance. At the beginning of our researches the European rabbit (*Oryctolagus cuniculus* Linné, 1758) had been the dominant herbivore species there, but as a result of two diseases in 1994 and 1995 they disappeared. Earlier studies had showed competition between these two species, therefore we expected a significant increase in the local hare abundance after the extinction of rabbits. Our results, however, did not comply with this supposition. Nonetheless, experimental comparison of the vegetation in grazed and ungrazed plots proved that rabbits had been significantly decreasing the vegetation cover, especially that of grasses; meanwhile hares did not. Although grasses were the main food components of both species, their moderate diet overlap throughout the year does not suggest a food competition between them. All these findings show that population size of hares was not significantly limited by rabbits due to trophic overlap. Competitive effect of rabbit on sympatric hares had been low or it was expressed by the depreciation of other non-investigated population characteristics.

Key words: *Lepus europaeus*, *Oryctolagus cuniculus*, population abundance, vegetation, diet

Introduction

In Europe (Mitchell-Jones et al. 1999, Edwards et al. 2000) and also in Hungary (Kovács & Heltay 1993, Csányi 1996) the number of European hares (*Lepus europaeus* Pallas, 1778) has declined continuously during the last decades. To stop this process and to elaborate a suitable management we need to gather more knowledge about the habitat and resource use of this species (Vaughan et al. 2003) and its interactions in the ecosystems (Broekhuizen 1975).

Food shortage is one of the main components in limiting the density of small herbivorous mammals, such as leporids (Gibb 1981). Density of leporids was found positively correlated with the biomass of herbaceous vegetation (MacCracken & Hansen

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1982). Consequently, a competitive interaction could take shape between leporids and other sympatric herbivorous species for the limited food resources (van der Val et al. 1998, Hulbert & Andersen 2001).

Several studies focused on the food competition between the European hare and European rabbit (*Oryctolagus cuniculus* Linné, 1758) (Homolka 1987a, Chapuis 1990). Besides that, the investigations also emphasize the importance of behavioural characteristics (Flux 1993, Stott 2003) and parasites (Broekhuizen 1975, Gilbert et al. 2001) in the competitive interactions between rabbits and hares. Numerous investigations noted a general increase in hare populations following the decline of rabbit population infected by myxomatosis (Moore 1956, Morel 1956, Rothschild 1961), which clearly suggests the interaction between them.

In our study area, in Bugac Juniper Forest of Hungary, we have carried out long-term ecological studies since 1990 (Altbacher 1998). There the European hare uses both the forest and the adjacent open field (Bíró & Altbacher 1996). According to radio telemetry studies of individuals caught in the forest, two different ranging strategies exist. Some individuals leave the forest for the open field during the nights to feed, while others always remain inside the continuous woody area.

Nevertheless, the European rabbit was the dominant species of this ecosystem. Its significant browsing effect on junipers in our study area has already been published (Mátrai et al. 1998). Heavy impact of its grazing was also clearly visible on the large open sandy grasslands between junipers (Kertész et al. 1993). In contrast to hares, rabbits never left the juniper forest; no occurrence of rabbits in the open field was detected (V. Altbacher, unpubl.). In 1994 and 1995 there were two diseases (myxomatosis and haemorrhagic disease) in the forest, followed by a very cold snowy winter. These facts together led to the extinction of the rabbit population in our study area.

Our long-term studies provided an opportunity to describe the spatiotemporal distribution of the European hare in the light of the changes in population density of the European rabbit. We investigated whether the local abundance of hares could have been limited by the presence of rabbits and primarily by the negative competitive effects due to significant trophic overlap. According to that our questions were:

- Did the abundance of the European hare increase after myxomatosis of rabbits?
- Did rabbits have a significant impact on the availability of plant species consumed by hares?
- How large was the overlap between the diet composition of hares and rabbits?

Study Area

The study area is located in the Bócsa-Bugac sandhill region belonging to the Kiskunság National Park, central Hungary (46°38'N, 19°40'E). It is basically covered by a juniper forest extending to 168 ha (1200 x 1400 m) and neighbouring open grassy areas (Fig. 1).

Bugac Juniper Forest consists of a mosaic of woods, shrubs and xeric grasslands lying on a sand dune system (Kertész et al. 1993). Woody areas are covered by planted black pine (*Pinus nigra*) and Scotch pine (*P. sylvestris*) forests or by differently composed stands of juniper (*Juniperus communis*), poplar (*Populus alba*, *P. canescens*), birch (*Betula pendula*) and black locust (*Robinia pseudoacacia*). Shrub patches are dominated by privet (*Ligustrum vulgare*), hawthorn (*Crataegus monogyna*), common barberry (*Berberis vulgaris*), sloe (*Prunus spinosa*), blackberry (*Rubus fruticosus*) and sallow (*Salix rosmarinifolia*). In

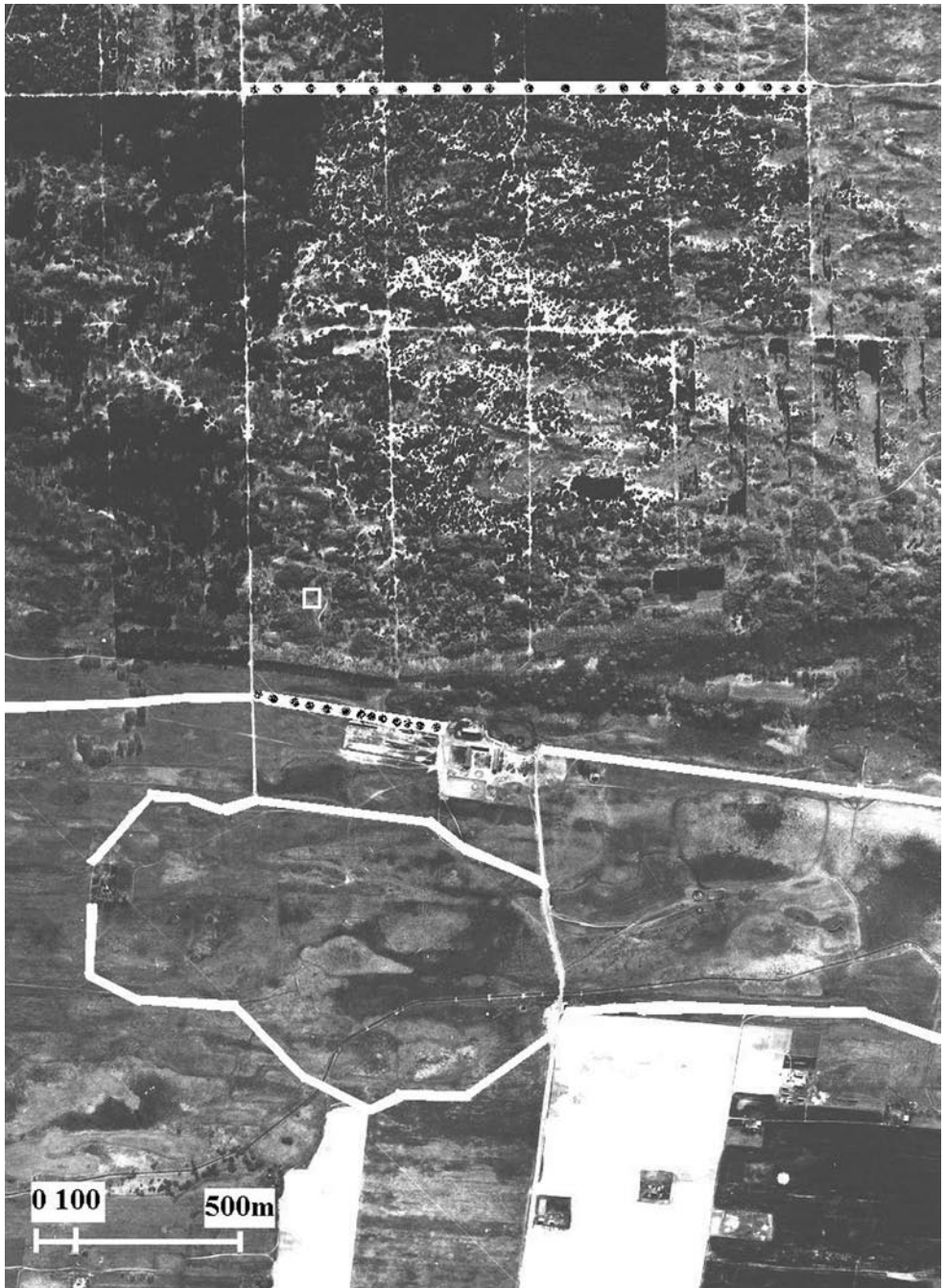


Fig. 1. Aerial photo of the study area. The mosaic of the juniper forest is represented on the upper half of the map, while the open sandy grassland on the lower one. Wide white lines show the permanent census lines (white – spotlighting transects, white with dark spots – track census lines). Study area in the forest, where faecal samples were collected, is located in the eight part of forest block bordered by dirty roads (thin white lines) between the two track census lines. Small square shows the site of permanent quadrates in the juniper forest. Large white blocks on the grassland are cultivated fields.

between woody patches intermediate open grassy patches are laid. Their typical herbaceous plant species are shown in Table 1.

Open areas are mainly sandy grasslands (K a t o n a et al. 2002), where the most common grasses are cheatgrass (*Bromus tectorum*) and fescues (*Festuca vaginata*, *F. rupicola*). Herbaceous plant species are similar to a great extent to those in the juniper forest. Some small patches of cultivated fields can also be found, mainly covered by alfalfa (*Medicago sativa*). Grasslands are intensively grazed by Hungarian gray cattle, sheep and horses. Consequently vegetation is generally short; grass height can range between 5 and 40 cm over the year.

Material and Methods

Population abundance estimations

Track density estimation

In every season of a given year between 1994 and 2000 track density estimation (P r a d a 2001) was carried out using one permanent dirt-road in the juniper forest and one at the forest-meadow boundary. We conducted estimations in the forest in every year and at the boundary in 1996, 1998, 1999 and 2000. Censuses were made for three consecutive days in the middle of January, April, July and October. The length of the forest line was 1400 m, while the edge line was 350 m. Censuses always started in early morning just after sunrise. The roads had been flattened the previous evening before sunset; therefore we could estimate the local track densities based on the night movements. All foottracks crossing the roads were recorded and the mammal species (European hare, rabbit, red fox, badger, polecat, roe and red deer, wild boar, dog and domestic cat) were identified. Although track density estimation is not a suitable technique for determining absolute population size, by this mean significant changes in population abundance can be easily detected in standardized conditions (L a n g b e i n et al. 1999).

Track densities of hares and rabbits were normalised to 1 km line length during the three days and averaged for obtaining seasonal data. Seasonal track densities within a year were used to estimate population changes by two-way repeated measures ANOVA (hare vs. rabbit by year). Differences between years were analysed for both species by Friedman-ANOVA. Changes in the abundance of hares leaving the forest at nights were also tested by Friedman-ANOVA based on the seasonal averages of track data collected at the edge-line of the forest.

Spotlighting

In every season of a given year between 1995 and 1999 spotlighting (F r y l e s t a m 1981) was carried out from a car using permanent roadlines in the open area. Censuses were made for three consecutive days in the middle of January, April, July and October. The study period always started the night before the track density estimations did. Spotlighting started consistently three hours after sunset and it lasted for one hour approximately. Five lines were designated at different distances from the edge of the forest. The total length of these lines was 7.1 km. Animals (European hare, roe deer and red fox dominantly) were identified from a car going at around 10 kilometers per hour. At least three observers were needed for

this estimation: a driver, who also had to watch animals crossing the road, and two people spotlighting both sides of the road. Spotlights with a light intensity of 500 000 candles were operated from the car battery. They enabled us to see animals within a range of 200 meters on both sides. We used strip-census estimates (P e p i n & B i r k a n 1981) on a standard area of 284 ha. When an animal was noticed, its species, distance from the starting point and from the actual road were recorded using a dictaphone. Records were put into writing after fieldwork.

Averaged hare densities of the three days normalised to 1 km line length gave the seasonal data. Seasonal densities within a year were used to compare years by Friedman-ANOVA.

V e g e t a t i o n a n a l y s i s

Between 1990 and 1999 permanent quadrates of 1 m by 1 m were subject to vegetation analysis in the forest. These quadrates were established to determine grazing effect of different herbivorous mammals on the grassy vegetation (H o l e c h e k et al. 1982). The study site of 0.25 ha was located in an open sandy grass patch inside of the forest, where a large rabbit colony lived and also hares occurred frequently. Quadrates were laid down systematically in a regular scheme of six lines with 2–2 treated and control plots. We had 24 quadrates altogether: 12 ungrazed quadrates enclosed and covered with a plastic mesh and 12 unprotected control plots accessible for grazers. Two surveys per year were conducted, one in late May and one in late September. We could not obtain suitable data for statistical analysis at all plots in 1993, and in autumn 1994 and 1999. Coverage of all plant species within the quadrates was estimated visually as a proportion of the total area (B r o w e s et al. 1998). Experienced standard observers with tested high interobserver reliability made coenological records.

Coverage and number of species of different plant groups (grasses, forbs, mosses, and lichens) were compared between grazed and ungrazed plots throughout the years by two-way repeated measures ANOVA. Differences between years were analysed by one-way repeated measures ANOVA with post-hoc Tukey-test for both treated and control group. Grazing effect was tested by independent samples t-test in each year. Statistical comparisons were carried out separately on data from May and September. Data distributions were always analysed using the Kolmogorov-Smirnov normality-test.

M i c r o h i s t o l o g i c a l f a e c e s a n a l y s i s

In 1995 and 1998 seasonal faecal pellet samples from hare and rabbit were collected in the juniper forest to determine the diet composition of leporids. In 1998 we could not find any rabbit faeces, which was a clear evidence of rabbit extinction. These collections were carried out during the same days that population density estimates were. Diet compositions were described by microhistological faeces analysis (B a u m g a r t n e r & M a r t i n 1939, D u s i 1949).

In all seasons composite samples of 10 independent pellets (200 m from each other at least) from both species were processed in the laboratory. Our earlier methodical investigations in this study area (K a t o n a & A l t b ä c k e r 2002) and several similar works support that this sample size is optimal for an accurate estimation (C h a p u i s 1980, H o m o l k a 1987b). Laboratory process was conducted as shown below (K a t o n a & A l t b ä c k e r 2002).

In every season for both species homogenized mixtures were prepared from the 10 pellets. Then 5 subsample of 0.01g were taken out into test tubes. After boiling in 20% nitric acid solution for 1.5 minutes epidermis fragments were dispersed on microscopical slides into a mixture of 0.1 ml of 87% glycerine and 0.05 ml of 0.1% Toluidine-Blue. We had altogether 5 slides from each seasonal sample of both leporids, on which all fragments found in a systematical manner were identified under 160x magnification. In each slide 100 plant epidermis fragments were identified. Proportion of plant species were estimated by the number of fragments for a particular forage type relative to the total number of fragments. In each case averages of 5 slides were used for further calculations.

χ^2 -tests of homogeneity were performed to compare diet composition between species, seasons and years. Diet overlap of rabbit and hare was calculated by Renkonen's similarity index (Hurlbert 1978):

$$Sis = \sum \min(P_{1,i} ; P_{2,i})$$

where $P_{1,i}$ is the proportion of plant category i in one species, $P_{2,i}$ in the other species.

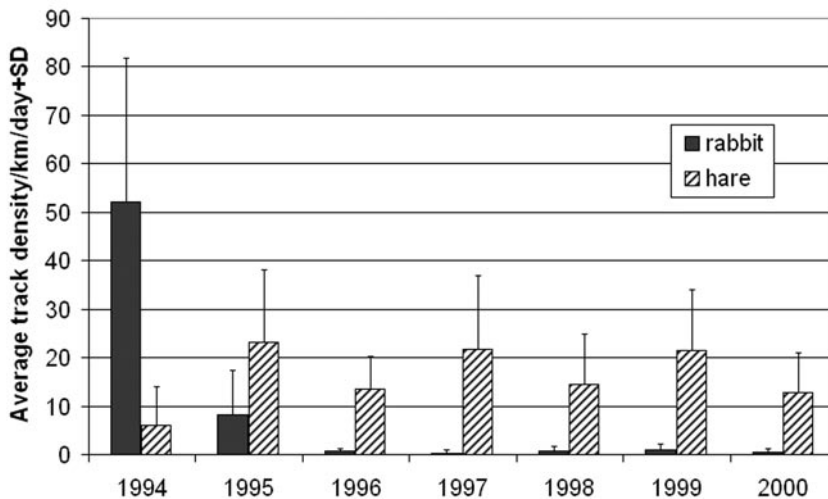


Fig. 2. Temporal changes in hare and rabbit abundance (mean±SD, n=4) in the juniper forest according to the track density estimation between 1994 and 2000.

Results

Population abundance estimations

According to track density estimations in the forest, rabbit and hare population abundance changed differently over the time (Two-ways repeated measures ANOVA: for years: $F(6,36)=4.38$ $p<0.005$, for species: $F(1,6)=3.03$, $p=0.13$, for interaction: $F(6,36)=9.94$, $p<0.001$). Rabbit abundance was much higher than that of hare before 1995. Then rabbit abundance significantly declined almost to 0 (Friedman ANOVA: $df=6$, $\chi^2=16.2$, $p<0.05$). Parallely, track density of hares rose after 1994, but there was no significant difference between years (Friedman ANOVA: $df=6$, $\chi^2=6.96$, $p=0.32$) (Fig. 2).

Table 1. Typical herbaceous plant species (>0.5%) in the intermediate open grassy patches in the juniper forest before (1990–1994, n=48) and after (1995–1999, n_{spring}=60, n_{autumn}=48) myxomatosis (mean coverage (%)). Coverage of mosses and lichens and number of species in different plant categories are also shown.

Plant species	1990–1994				1995–1999			
	Spring		Autumn		Spring		Autumn	
	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed
Grasses	20.44	35.63	28.39	49.98	50.62	43.57	50.97	45.72
<i>Bromus tectorum</i>	0	0	0	0	0	0.83	0	0
<i>Calamagrostis epigeios</i>	0	5.74	0	3.67	3.64	2.67	2.98	1.62
<i>Carex liparicarpos</i>	19.59	28.29	26.46	39.21	44.44	38.04	46.00	42.83
<i>Carex stenophylla</i>	0	0	0	0	0.57	0	0.01	0
<i>Koeleria glauca</i>	0	0	0	0	0.57	0	0.37	0
<i>Poa bulbosa</i>	0	0	0	0	0.53	0	0.13	0
<i>Stipa</i> spp.	0	0	0	0	0.73	0	0.07	0
<i>Tragus racemosus</i>	0.01	0	1.47	4.72	0	0	0	0
Forbs	7.64	12.18	6.40	9.11	19.65	24.7	7.19	10.75
<i>Alyssum</i> spp.	0	1.02	0	0	0	0	0	0
<i>Alkanna tinctoria</i>	0	0.12	0	1.32	0	1.25	0	0.29
<i>Anchusa officinalis</i>	0.91	0	0.14	0	1.89	4.02	0.24	1.04
<i>Arenaria serpyllifolia</i>	0.59	1.29	0.02	0.02	1.43	0.79	0.01	0.02
<i>Calamintha acinos</i>	0	0	0	0	0	1.11	0	0.54
<i>Crepis rhoedifolia</i>	0	0	0	0	0	0.19	0	0.02
<i>Erigeron canadensis</i>	0	0	0	0	1.22	1.82	1.88	2.41
<i>Eryngium campestre</i>	0	0	0	0	2.03	2.10	0	0.05
<i>Euphorbia cyparissias</i>	0	0	0	0	0.75	0	1.26	0
<i>Galium aparine</i>	0	0	0	0	1.21	0.92	0.13	0.56
<i>Linum hirsutum</i>	0.37	1.13	1.09	2.03	2.09	0.73	0.63	0.48
<i>Myosotis arvensis</i>	0.78	0	0	0	0	0	0	0
<i>Teucrium chamaedrys</i>	2.27	2.02	4.61	2.35	3.87	6.50	2.32	4.43
<i>Thymus glabrescens</i>	0	0.77	0	0	0	1.22	0	0
<i>Veronica arvensis</i>	0.84	0	0	0	1.18	0	0	0
<i>Viola kitaibeliana</i>	0.82	2.37	0.02	0.02	1.77	2.93	0.03	0.06
<i>Juniperus communis</i>	1.80	0	3.50	0	6.10	1.16	2.68	0.93
Mosses	11.88	9.47	6.85	7.77	28.1	31.99	14.19	21.39
<i>Hypnum cupressiforme</i>	0.56	0	0.37	0	1.53	0	1.33	0
<i>Tortella inclinata</i>	2.58	0.94	1.89	0.20	2.40	4.79	2.50	4.77
<i>Tortula ruralis</i>	8.73	8.54	4.59	7.57	24.17	27.19	10.36	16.62
Lichens	3.13	2.21	3.93	1.98	2.58	5.21	1.57	1.90
<i>Cladonia furcata</i>	0.37	0	1.11	0	0	0.60	0	0.25
<i>Cladonia magyrica</i>	2.41	0	2.48	0	0.85	0.56	0.97	0.41
<i>Cladonia convoluta</i>	0	1.74	0	1.61	1.42	3.51	0.39	0.89
Total coverage	29.91	47.81	38.29	59.09	76.03	69.42	60.53	57.41
Grass species	2.50	2.35	2.23	2.37	2.24	2.31	2.08	2.03
Forb species	5.54	5.83	2.52	3.12	4.68	4.56	2.45	2.43
Moss species	1.35	1.33	1.02	0.98	1.29	1.33	1.02	1.05
Lichen species	2.06	2.00	2.17	2.12	1.50	1.86	1.57	2.00

Table 2. Changes in the abundance of rabbits and hares in the forest and at the edge of the forest (number of tracks/km/day, mean±SD, n=3) and in the open grassy area (number of individuals/100 ha/day, mean±SD, n=3) between 1994 and 2000. In empty cells no data are available.

Year	Season	Forest		Edge		Grassland	
		Rabbit (track/km/day)	Hare (track/km/day)	Rabbit (track/km/day)	Hare (track/km/day)	Rabbit (individual/100 ha/day)	Hare (individual/100 ha/day)
1994	winter	65.00 (43.47)	3.33 (1.09)				
	spring	85.95 (17.27)	1.67 (1.80)				
	summer	17.50 (0.51)	1.07 (0.51)				
	autumn	40.00 (26.96)	17.86 (22.15)			0	7.16 (0.54)
1995	winter	21.79 (17.68)	34.29 (31.31)			0	4.11 (3.61)
	spring	2.86 (3.11)	37.86 (11.80)			0	2.00 (0.41)
	summer	2.62 (2.06)	11.90 (4.65)			0	2.35 (1.63)
	autumn	5.48 (1.09)	8.57 (3.71)			0	3.17 (0.35)
1996	winter	1.19 (1.09)	8.33 (2.97)	0	36 (18.25)	0	4.34 (1.33)
	spring	0.95 (0.41)	20 (4.29)	0	111 (31.75)	0	1.17 (0.41)
	summer	0.48 (0.82)	18.57 (4.68)	0	15 (12.00)	0	1.17 (1.13)
	autumn	0	7.38 (6.24)	0	35 (4.58)	0	2.00 (1.47)
1997	winter	0	2.62 (3.30)			0	2.58 (1.08)
	spring	0	29.52 (21.07)			0	1.29 (0.20)
	summer	0	34.52 (26.19)			0	1.17 (0.20)
	autumn	1.19 (0.82)	22.38 (9.70)	0	78 (64.13)	0	2.46 (1.86)
1998	winter	0.71 (1.24)	18.81 (3.60)	0	31 (4.58)	0	0.82 (0.41)
	spring	2.14	26.43 (15.67)	0	13 (1.73)	0	1.29 (0.54)
	summer	0.24 (0.41)	10.24 (1.09)	0	13 (13.53)	0	0.82 (0.20)
	autumn	0	2.38 (2.18)	0	22 (6.24)	0	3.87 (0.61)
1999	winter	0	17.38 (12.80)	0	60 (16.70)	0	1.06 (0.70)
	spring	2.38 (0.82)	40.00 (21.62)	0	26 (9.64)	0	1.53 (1.47)
	summer	1.43 (2.47)	16.90 (5.46)	0	32 (1.73)	0	0.82 (0.41)
	autumn	0	11.43 (1.89)	0	11 (9.17)	0	3.64 (2.00)
2000	winter	0	7.14 (4.29)	0	13 (15.39)		
	spring	1.43 (1.24)	24.29 (15.45)	0	26 (13.53)	0	3.17 (0.61)
	summer	0	13.10 (2.18)	0	27 (13.75)	0	2.93 (0.41)
	autumn	0.48 (0.82)	6.19 (4.06)	0	14 (6.24)	0	3.99 (1.08)

At the same time hare abundance has not increased in the field, either, but has been stable based on spotlighting (Friedman ANOVA: df=4, $\chi^2=3.38$, p=0.5). While, according to track density estimations at the edge of the forest, number of hares leaving the forest at nights has not changed significantly, in fact a slight decreasing tendency could be detected (Friedman ANOVA: df=3, $\chi^2=3.46$, p=0.33) (Table 2).

Vegetation analysis

Total vegetation coverage of both kinds of sample plots significantly changed over the years; it was significantly higher in ungrazed than in grazed plots before rabbit extinction, but not after (Two-ways repeated measures ANOVA: spring: for years: F(8,176)=46.13 p<0.001, for grazing: F(1,22)=0.17, p=0.687, for interaction: F(8,176)=2.85, p<0.005; autumn: for years: F(6,132)=16.74 p<0.001, for grazing: F(1,22)=0.86, p=0.36, for interaction: F(6,132)=4.51,

$p < 0.001$; one-way repeated measures ANOVA between years within treatments: $p < 0.001$ in all cases; independent samples t-tests between treatments: $p < 0.05$ only between 1990 and 1992).

Similar temporal changes were found in the coverage of grasses (Two-ways repeated measures ANOVA: spring: for years: $F(8,176)=22.9$ $p < 0.001$, for grazing: $F(1,22)=0.33$, $p=0.57$, for interaction: $F(8,176)=4.64$, $p < 0.001$; autumn: for years: $F(6,132)=10.32$ $p < 0.001$, for grazing: $F(1,22)=2.61$, $p=0.12$, for interaction: $F(6,132)=6.47$, $p < 0.001$; one-way repeated measures ANOVA between years within treatments: $p < 0.001$ in all cases; independent samples t-tests between treatments: $p < 0.005$ only between 1990 and 1992) (Fig. 3).

Coverage of forbs, mosses and lichens and number of species changed along the years, but there was no grazing effect (Two-ways repeated measures ANOVA: for years: $F(8,176)$, $p < 0.05$, for grazing: $F(1,22)$, $p > 0.25$, for interaction $F(6,132)$, $p > 0.05$) (Table 1).

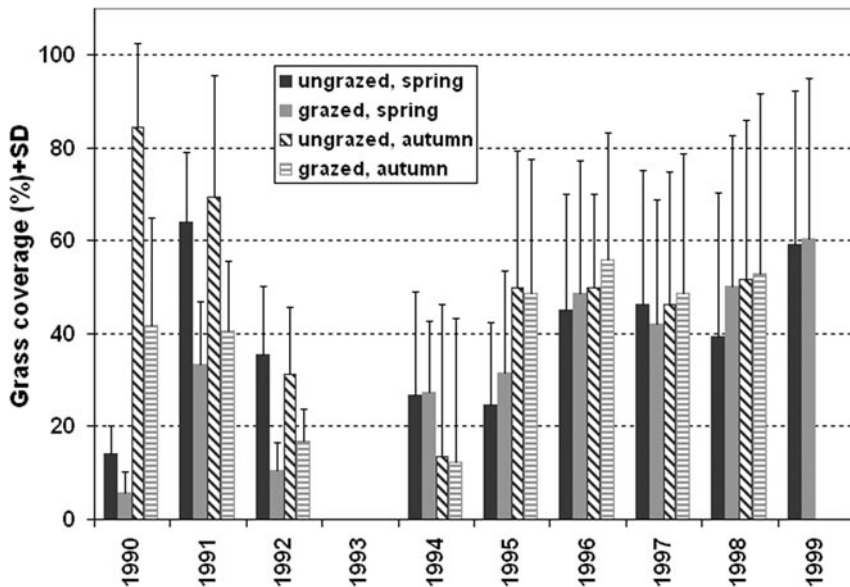


Fig. 3. Grazing impact of rabbits and hares on the grass coverage (mean±SD, n=12) in the juniper forest according to the vegetation analyses between 1990 and 1999.

Diet composition analysis

Diet composition of hares was significantly different from that of rabbits in all seasons in 1995 as well as in 1998 (χ^2 -test: $df=4$, $p < 0.05$, except autumn in 1995 ($p > 0.1$)). Nevertheless, grasses were the most important diet components for both species for most of the year (Table 3).

Proportional similarity between rabbit and hare diet was relatively high in autumn, intermediate in summer and winter, while in spring similarity was high for plant categories, but low for species (Table 4).

Diet composition of both species significantly changed over seasons (χ^2 -test: $df=12$, $p < 0.005$). There was also a clear alteration in the food composition of hare between 1995 and 1998 (χ^2 -test: $df=4$, $p < 0.005$). Grass consumption of hares increased in summer and winter after rabbit extinction (Table 3), but it decreased in spring. Diet composition of hares in 1998 did not show much higher similarity to the diet of rabbits, than that of hares in 1995 (Table 4).

Table 3. Diet composition (occurrence %) of hare and rabbit in the juniper forest in different seasons (Spr-spring, Sum-summer, Au-autumn, W-winter) in 1995 and 1998.

Plant species	Rabbit 1995				Hare 1995				Hare 1998			
	Spr	Sum	Aut	W	Spr	Sum	Aut	W	Spr	Sum	Aut	W
Grasses	83	25	60	49	91	7	72	22	65	56	64	52
<i>Elymus</i> spp.	71	25	8	0	22	0	9	4	1	10	22	1
<i>Asparagus officinalis</i>	0	0	0	0	0	7	0	0	0	1	1	0
<i>Bromus squarrosus</i>	12	0	34	34	18	0	32	12	35	13	23	37
<i>Carex</i> spp.	0	0	4	2	0	0	1	0	0	2	1	1
<i>Cynodon dactylon</i>	0	0	0	0	20	0	0	0	0	0	0	0
<i>Festuca</i> spp.	0	0	13	9	0	0	30	3	27	24	14	13
<i>Phleum phleoides</i>	0	0	0	0	30	0	0	0	0	0	0	0
Other grasses	0	0	1	4	1	0	0	3	2	6	3	0
Forbs	9	44	14	1	9	81	12	2	2	16	5	3
<i>Alyssum</i> spp.	0	0	2	0	0	0	5	0	1	0	0	1
<i>Cenchrus incertus</i>	0	0	0	0	9	9	0	0	0	0	0	0
<i>Chaenopodium</i> spp.	7	10	0	0	0	13	0	0	0	0	0	0
<i>Conyza canadensis</i>	2	27	0	0	0	35	0	0	0	0	0	0
<i>Medicago sativa</i>	0	0	0	0	0	12	0	0	0	0	0	0
<i>Potentilla arenaria</i>	0	7	2	0	0	0	3	0	0	0	0	1
<i>Saponaria officinalis</i>	0	0	0	0	0	6	0	0	0	0	0	0
<i>Thymus glabrescens</i>	0	0	1	0	0	6	0	0	0	4	0	0
Other forbs	0	0	9	1	0	0	4	2	1	12	5	1
Browses	8	9	25	46	0	5	15	50	26	16	20	37
<i>Berberis vulgaris</i>	0	0	6	4	0	0	8	0	4	3	3	6
<i>Ligustrum vulgare</i>	0	0	3	9	0	0	2	8	12	9	3	11
<i>Populus alba</i>	0	9	0	0	0	0	0	0	0	0	0	0
<i>Salix repens</i>	0	0	0	0	0	5	0	0	0	1	3	1
<i>Sambucus</i> spp.	8	0	2	2	0	0	0	0	1	1	0	0
Unidentified barks	0	0	14	31	0	0	5	42	9	2	11	19
<i>Juniperus communis</i>	0	22	0	1	0	6	0	23	5	0	1	5
Seeds	0	0	0	1	0	0	0	4	2	11	9	3
Unidentified epidermis	0	0	1	2	0	0	1	0	1	1	1	1

Table 4. Diet overlap between rabbit and hare in 1995 and between 1995 and 1998 estimated by Renkonen's proportional similarity index in the juniper forest in different seasons. Values were calculated using plant species and plant categories, as well.

Season	Rabbit 1995 – Hare 1995		Hare 1995 – Hare 1998		Rabbit 1995 – Hare 1998	
	plant species	plant groups	plant species	plant groups	plant species	plant groups
spring	0.34	0.92	0.19	0.66	0.14	0.75
summer	0.43	0.63	0.05	0.28	0.1	0.5
autumn	0.74	0.88	0.6	0.85	0.66	0.86
winter	0.49	0.64	0.5	0.6	0.76	0.89

Discussion

During our long-term studies the extinction of rabbits was an unexpected event. Consequently, we had no opportunity to test competition between the two leporid species in a classical experimental manner. But taking advantage of rabbit extinction, we could compare the situation before and after that. Forsyth & Hickling (1998) e.g. proved interspecific competition between two herbivorous species based on their adverse density changes in a comparative study of allopatric and sympatric populations.

Our studies did not show the same significant increase in hare abundance after the decline of rabbit population that had been noted by others (Moore 1956, Morel 1956, Rothschild 1961). It rather corresponds to Vaughan et al. (2003), who did not find any relationship between the occurrence of hares and that of rabbits. Similarly, Barnes & Tapper (1986) also stated that there is no casual relationship between the abundance of the two species. Our result, therefore, shows that abundance of the European hare was not limited by the presence of the European rabbit. Nevertheless, we have to consider the possibility, that high seasonal and yearly natural fluctuations of hare abundance (Kovács & Helty 1993) could cover the manifestation of competitive effects.

Investigation of competition is generally based on determination of niche overlap and not on field experiments (Schoener 1983). However, resource overlap alone does not measure the amount of competition, since the availability of resources and niche-segregation should also be considered (Sale 1974). In a comparative study on the diet of rabbit and hare (Homolka 1987a) these leporids were considered as evident trophic competitors after a result of 49–78 percent of overlap. Contrarily, Chapuis (1990) had an opposite conclusion upon similar results, that is, the two leporids did not compete for food. But that study was carried out in an agroecosystem, where the plants eaten were available in excess.

Our results, in agreement with Forgeard & Chapuis' results (1984), clearly showed the strong grazing effect of rabbits, especially on the availability of grasses. Dietary studies demonstrated that grasses were important components in the food of hares in both years, too; just like in other areas (Homolka 1982, Hulbert et al. 2001). It could potentially lead to competition for forages, but to prove this statement we need evidence that availability of grasses was limited for hares. Our data on the vegetation give only suggestions for that. Furthermore, diet composition of hares is influenced by individual (Katoná & Altbäcker 2002), temporal and spatial variability (Homolka 1987c). Although we could partly control them, they made the niche-overlap determination uncertain. Fecal analysis generally overestimates grass and browse species and underestimates forbs due to differential digestibility of these foods (Smith & Shandruk 1979, Holeček et al. 1982) Contrarily, other studies suggest digestion only causes a slight difference in detecting plant composition of herbivore diets (Hansen et al. 1973, Johnson & Wofford 1983). Some plant species, which were intensively consumed by hares, were scarce in the forest and abundant in the open grassland (e.g. *Bromus* sp.) This fact shows that a significant part of hare population leaves the forest for the open field during the nights to feed. Hare individuals following this shifting strategy could suffer less competition than resident ones. Likewise, on the basis of the moderate diet overlap food competition could not be considered to be important. The fact, that after the extinction of rabbits hare diet did not shift significantly towards the earlier diet composition of rabbits also tells against a considerable food competition.

Though, neither changes in the abundance of hares, nor the extent of trophic overlap could support the importance of interspecific competition between hares and rabbits; we have to consider the role of some other factors. We can not exclude the possibility that hares were influenced by rabbits through a non-investigated mechanism and/or the competitive effects were expressed in the failure of other population characteristics (e.g. condition, breeding success). F l u x (1993) stated that competition between hares and rabbits includes a combination of factors, such as food competition, rabbit parasites or simple aggressive behaviour. B r o e k h u i z e n (1975) concluded that stomach worm (*Graphidium strigosum*) is an original parasite of rabbits, which only harms less-adapted hares in the presence of rabbit. Nevertheless, they rejected that hares are driven out by aggressive behaviour of rabbits. They noted that less than one percent of interspecific encounters ended by a rabbit attack. Contrarily F l u x (1981) argued that rabbits dominate hares in these cases.

Summarizing, in our studies we did not find a clear indication, that local abundance of the European hare was significantly limited by the exploitation of similar food resources by the European rabbit. We consider the European rabbit as a fundamental species of Bugac Juniper Forest, that determined significantly the actual features of the vegetation by its grazing. However, competitive effect of rabbit on sympatric hares had been low or it was expressed by the depreciation of other non-investigated population characteristics. To preserve the unique landscape of Bugac Juniper Forest and slow down the succession process a controlled reestablishment of rabbit population in the juniper forest would be required. Nevertheless, before any intervention the effect of rabbits on the herbivore community, and especially on hares should be also considered.

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