Seasonal home range shift of red deer hinds, *Cervus elaphus*: are there feeding reasons?

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Abstract. This work shows records of seasonal home range shift of radio collared red deer hinds (*Cervus elaphus* L., 1758) in southern Hungary from a forested block to the surrounding agricultural area every June between 1994–2000. Better quality of agricultural than forest forages is suggested as the main reason for this shift. Two hypotheses were tested: i) red deer consume mainly cultivated plants in the agricultural area and ii) agricultural plants are more nutritious than those in the forest at the time of home range shifting. Composition of forest and agricultural diet was determined by microhistological faeces analysis and the nutritive quality was assessed by the amount of crude protein and crude fibre content. Red deer diet was dominated by browse in the forest (65–85 %) whilst, in agricultural fields, wood species were as important as grasses (26–44 and 39–55 %, respectively). Consumption of cultivated plants was low (under 10 %) in the agricultural area. Nutritive quality of the diet was lower at the agricultural site than in the forest due to lower crude protein and higher crude fibre content. Seasonal home range shift of red deer hinds therefore, could not be explained by better nutritive quality of agricultural plants only. We suggest other factors that could potentially explain this behaviour.

Key words: diet composition, habitat change, nutritive quality, faeces analysis, forest-agriculture habitat

Introduction

Red deer (*Cervus elaphus* L., 1758) home range has been investigated in several studies (Georgii 1980, Georgii & Schröder 1983, Catt & Staines 1987, Clutton-Brock & Albon 1989, Carranza et al. 1991, Szemethy et al. 1998). Differences in study areas implied diversified behaviour of red deer. For instance, a strong site-fidelity by female red deer was shown in Scotland (Catt & Staines 1987, Conradt et al. 1999).

Several studies have shown a seasonal home range shift of large herbivores (Escos & Alados 1992, Borkowski & Furubayashi 1998). For instance, studies on North-American white-tailed deer (*Odocoileus virginianus*) (Kammermeyer & Marchinton 1976) found long-distance seasonal movements in stags and suggested that this was due to the intrasexual competition. The same was argued for the dispersion of red deer stags by Bobek et al. (1987). In red deer hinds, however, seasonal changes in availability of food were invoked as the main reason explaining alteration of habitat use (Georgii 1980, Schmidt 1993).

Radiotelemetry studies conducted in our study area since 1994 (Szemethy et al. 1998) have shown a seasonal home range shift in 9 of 27 radio collared red deer hinds. The remaining part of the marked hinds stayed stable in the forest throughout the year. These

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data were further supported by track and bed counts as well. Local game managers and hunters made similar observations in unmarked animals. Weekly daylight localisation over the years showed that red deer hinds shifted their home range from the forest to the neighbouring agricultural fields in early summer, returning to the forested areas by late autumn. The average distance between forest and agricultural home range fragments was 8.9 ± 2.03 km (x ± SD), whilst the average action radius was only 2.6 ± 1.0 km for them. Observations during 24 h periods showed that there were no daily movements between the forest and agricultural area (S z e m e t h y et al., unpublished data).

This home range shift means a single long-distance movement from a well-known habitat to an area with unfamiliar current conditions across a highway and in close proximity to human settlements. It is a home range shift involving a high risk and energy cost, which should therefore be balanced by significant benefits. Differences among habitats in availability of food (G e o r g i i 1980, S c h m i d t 1993) is a common reason for larger movements of red deer hinds and stags. O s b o r n & J e n k s (1998) have already noticed, that white-tailed deer density was twice higher in areas with access to agricultural land, suggesting that these fields are important feeding sites. Reports of local game managers on significant damages to crops caused by red deer in the agricultural fields also confirmed use of agricultural fields. Our first hypothesis in the present study was that red deer consume primarily cultivated plants after shifting home range and as a consequence, food selection will also change in this period. Foraging on a diet of better quality (A l b o n & L a n g v a t n 1992) could also be an important reason for seasonal movements. Hinds need an increase in protein intake during the suckling period (C l u t t o n - B r o c k & A l b o n 1989). Therefore, our second hypothesis was that a better quality of agricultural than forest plant food could contribute to explain seasonal home range shift between forest and agricultural habitat.

The large scale intensive afforestation program in the Hungarian lowlands in the near future will result in expansion and dominance of agriculture-forest mosaics. Therefore, understanding this seasonal habitat change between forest and agricultural fields is necessary for both successful wildlife management and the mitigation of damage to agricultural crops. For testing our hypotheses we compared red deer diet composition and quality between habitats during the period of shifting.

Study Area

The study was carried out in the Hungarian Great Plain, at Hajósszentgyörgy, South Hungary (46°24' N, 19°70' E). The study area (40 000 ha) is a sand hill region composed of a large forest tract (14 600 ha) surrounded by extensive agricultural fields. Soil is chalky sand in the forest and sodic in agricultural areas. The forest is settled and is under intensive management (human-made forest plantations, clearings, enclosures and logging). The dominant tree species are black-locust (*Robinia pseudoacacia*) (54%) and pine (*Pinus silvestris* and *P. nigra*) (32%). Very dense shrub cover could be found inside 30% black-locust forests dominated mainly by hawthorn (*Crataegus monogyna*) (94%), elder (*Sambucus nigra*) (17%) and blackthorn (*Prunus spinosa*) (31%). Conversely, a great part of these forests (70%) has no understorey. In pine forests western hackberry (*Celtis occidentalis*) is predominant (20 %) and shrubless pine compartments are also frequent (14%). The forest area is separated from the neighbouring agricultural land by a highway (Fig. 1).

The agricultural area consists of cultivated fields (72%) and patches of reedy (*Phragmites communis*) and goat-willow (*Salix caprea*)-poplar (*Populus* sp.) groves (20%) along channels. Wheat (*Triticum aestivum*, 36%) and maize (*Zea mays*, 32%) are the most common cultivated plants. Fields of alfalfa (*Medicago sativa*), sunflower (*Helianthus annuus*) and barley (*Hordeum vulgare*), as well as private fields and small scattered meadows cover 10 % of the area. The average precipitation varies between 530–620 mm a year, whilst yearly mean temperature is 10.7 °C.

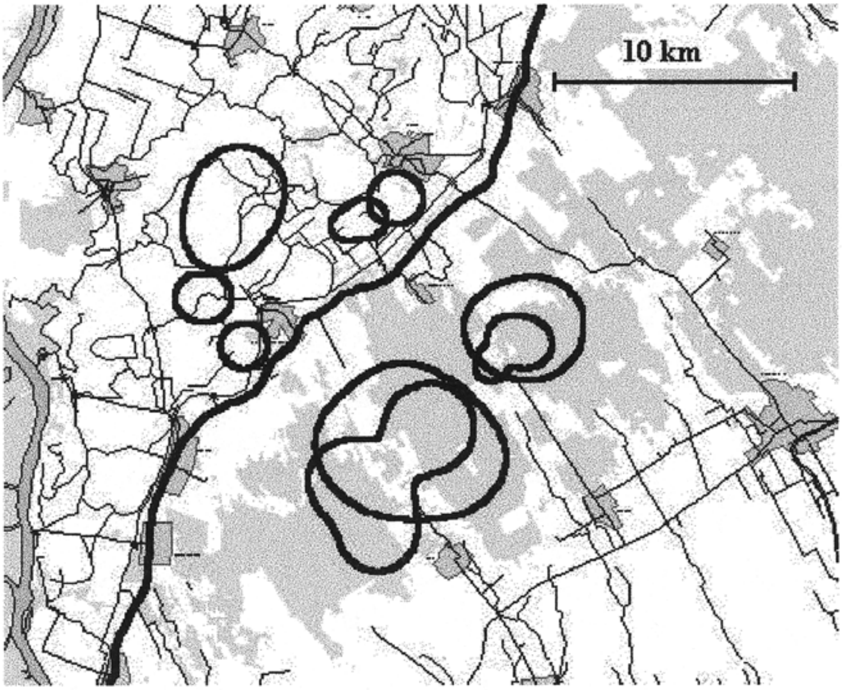

Fig. 1. Map of study area. Forested areas are grayish and agricultural fields are white. Human settlements are also shown by gray patches. Wide black line shows the highway between habitats and thinner lines the other small roads. Seasonal home range fragments of some shifter red deer are also provided by areas bordered with wide black lines.

Material and Methods

F o r a g e   a v a i l a b i l i t y

To characterise food availability vegetation analyses were carried out in the areas intensively used by radio tracked red deer since 1994. Percent coverage of dominant forages was estimated using an actualised vegetation map showing the different vegetation patches for both habitats (as shown above). We completed this map by field vegetation sampling in 500 and 100 ha forest and agricultural areas, respectively. Seventeen permanent plots of 10 m^2 were established in parallel lines (4–5 plots per line), located 500 m from each other in the forest; and 13 quadrates of 0.25 m^2 placed systematically in two lines (6–7 plots per line), 100 m from each other in the agricultural field. Vegetation of both habitats was sampled once in a fortnight between 15 June–15 July of 2000 (3 times altogether). This period includes the observed times of home range shifting from the forest to the agricultural area.

The main goal of this forage availability measure was to determine the preference for broad forage groups (grasses, forbs, browses) in both habitats and for cultivated plants in the agricultural area. Resolution of our sampling was adjusted to this aim. Vegetation map provided us enough information on abundance of browses and cultivated plants. Additional field vegetation sampling was carried out to estimate the abundance of different tree and shrub species in the forest; while abundance of different herbaceous plant species was only determined by this method in a meadow of the more homogenous agricultural field.

Diet composition

Diet composition of red deer was determined by microhistological analysis of faeces (Dusi 1949, Mátrai & Kabai 1989, Katona & Altbäcker 2002). Between 16 to 24 droppings were collected in both areas simultaneously with vegetation sampling (23, 16, 18, 24 droppings in the forest and 23, 16, 23, 24 droppings in the agricultural land, on 15 June,1998 and 15 June, 30 June, 15 July, 2000, respectively). Faecal pellets were kept in a freezer at -20 °C until further analyses. Then the following technical process was carried out.

Frozen droppings were defrosted at a temperature of 25 °C. Composite faecal samples were made for both areas for each sampling period by taking out five pellets from each pellet group. Three g of these homogenised mixtures was boiled in 200 ml of 20% HNO_3 for 4 minutes. Epidermis fragments were removed and dispersed into a mixture of 0.1 ml glycerine and 0.05 ml of 0.2 % Toluidine-Blue and placed in slides. Microscopic slides were covered and examined by systematic scanning under 400X magnification. One hundred epidermis fragments were identified on the slides using a reference collection of plant species collected from the study area (Mátrai et al. 1986). Proportions of diet components were estimated from the number of fragments for a particular forage class relative to the total number of fragments.

Data collected at three sampling times in 2000 were averaged. χ^2 homogeneity tests were performed to compare the diet composition (for broad forage groups: browse, forbs, grasses) of red deer broken down by habitats and years. Comparison between years was performed using data of sampling on 15 June in both years. χ^2 goodness of fit test and Bonferroni Z-test (Byers et al. 1984) were used to compare the proportion of different forage groups within habitats. Diet diversity was expressed by the Shannon-Weaver index (Shannon & Weaver 1949), while dietary preferences by the Ivlev-index (Ivlev 1961):

$$PI = (a-b) / (a+b)$$

in which a is proportion of a plant species in the diet and b is proportion of a plant species in the foraging area.

Significance of dietary preferences was tested by Bonferroni Z-test. Evenness of diet was also estimated by using the ratio between diet diversity and the logarithm (ln) of the number of consumed species (Sexson et al. 1981).

Nutrition quality

Nutritive quality of the diet was compared between forest and agricultural sites in 1998 and 2000. In each sampling time samples of plant species occurring at abundance of over 5 % in the diet (based on our preliminary studies) were collected in both habitats. Field observations showed that red deer consume young leafy sprigs of shrubs and trees and above ground parts of herbaceous plants and they are not able to select for leaves and avoid stems. Thus, bulked samples of leave and stem were collected as simulating bites taken by deer during its feeding behaviour. Pilot studies revealed that nutritive composition of a plant species is very homogenous in the entire forest-agriculture complex in a given time (O r o s z , unpublished data). According to that one sample of 300 g from each plant species was collected in each sampling time and kept in a freezer at -20 °C until further analysis.

Samples were oven-dried for 4 hours at 105 °C to determine total dry matter content and then ground to 1 mm size. These samples were analysed for crude protein and crude fibre, additionally crude fat, crude ash and nitrogen-free extracts according to the Weende-method (C h u r c h & P o n d 1988).

Although it could be an alternative method for estimating diet quality, digestive energy content was not measured because of its significant difficulties and unreliability when used in free-ranging animals (R o b b i n s 1993). Nevertheless, many studies apply nutritive components (especially crude protein and crude fibre content) as main determinants of diet quality (G r e e n 1987, C h e n et al. 1998). Diet in the agricultural area was considered better if its crude protein content was significantly higher and the crude fibre content significantly lower than diet in the forest area. Since digestible energy and protein could be used as a currency (B e r t e a u x et al. 1998, V a n d e r W a l et al. 2000), our approach could reveal whether significant difference in diet quality between areas exists.

Red deer diet was prepared by mixing collected plant species in the same proportion as the averaged estimated in faeces analysis and this mixture was analysed for its nutritive quality. Nutritive values of diet in the forest and agricultural sites were calculated for each sampling time. χ^2 homogeneity tests and Bonferroni Z-test were performed to compare the nutritive composition of diet (amount of crude protein, crude fibre, crude ash, crude fat content and N-free extracts for a given amount of food intake) by habitats and years using data of sampling on 15 June in both years.

Results

In both years overall diet (browse, forbs, grasses) of red deer significantly differed between the two habitats (χ^2 homogeneity test: df=2, χ^2=74.29, $p<0.005$ in 1998; df=2, χ^2=27.9, $p<0.005$ in 2000) (Table 1). Grasses were consumed to much greater extent, while woody species in much lower proportion in the agricultural area than in the forest. The difference between years in the diet composition, however, was not significant for broad forage groups (χ^2 homogeneity test: forest: df=2, χ^2= 3.7, $p>0.05$; agricultural area: df=2, χ^2=1.08, $p>0.05$).

In the forest red deer consumed predominantly browse species over grasses and forbs (χ^2 goodness of fit test: df=2, χ^2=55.32, $p<0.005$ in 1998, df=2, χ^2=26.29, $p<0.005$ in 2000). Preference of browses and primarily that of locust was high ($p<0.05$) (Table 2).

In the agricultural area browse species and grasses were foraged in higher proportion than forbs (χ^2 goodness of fit test: df=2, χ^2=10.09, $p<0.01$ in 1998, df=2, χ^2=7.97, $p<0.05$ in 2000). However, browses were preferred in this habitat, while grasses were avoided ($p<0.05$).

Consumption of cultivated plants was low, red deer selected significantly fewer cultivated plants than expected (χ^2 goodness of fit test: df=1, χ^2=71.45, $p<0.005$ in 1998, df=1, χ^2=95.27, $p<0.005$ in 2000). Alfalfa and wheat each made up 6 % of the agricultural

Table 1. Proportion (%) of plant groups and dominant plant species in red deer diet in the forest and in the agricultural area. In 1998 values were determined from the faecal samples collected on 15 June, while in 2000 results of three samplings (15 and 30 June, 15 July) were averaged (SD in bracket).

Plant species	Forest area		Agricultural area	
	1998	2000	1998	2000
Browse	**85**	**65 (23.7)**	**26**	**44 (18.5)**
Celtis occidentalis	3	9 (9.3)	0	0
Pinus spp.	33	0	0	0
Prunus spinosa	13	5 (4.8)	0	3 (2.5)
Robinia pseudoacacia	14	33 (14.6)	0	0
Rubus spp.	2	3 (2.5)	0	6 (5)
Salix caprea	0	2 (2.9)	22	30 (26.7)
Sambucus nigra	7	10 (2.3)	4	2 (2.1)
Others	13	3	0	3
Forbs	**9**	**27 (16.6)**	**19**	**16 (10.7)**
Ballota nigra	0	7 (11.4)	0	0
Medicago sativa	1	16 (3.9)	6	4 (2.5)
Ranunculus spp.	0	0	7	0
Others	8	4	6	12
Grasses	**6**	**8 (7.2)**	**55**	**39 (15.3)**
Agropyron repens	2	0	18	10 (9.5)
Agrostis alba	0	0	5	0
Carex spp.	0	1 (0.5)	12	1 (0.6)
Festuca spp.	0	1 (2.3)	0	23 (11)
Phragmites communis	0	0	11	0
Triticum aestivum	0	0	6	0
Others	4	6	3	5
Seeds	**0**	**0**	**0**	**1 (2.3)**

Table 2. Forage availability in the vegetation (VEG), proportion of dominant plants (>5%) in red deer diet (DIET) and preference indices (PI) calculated in the forest and agricultural area in early summer, 2000 (*= significant PI, p<0.05). Average proportion of plant categories is given by results of three samplings (15 and 30 June, 15 July).

Dominant plants	Forest area			Agricultural area		
	VEG	DIET	PI	VEG	DIET	PI
Browse	**48**	**65**	**0.16**	**11**	**44**	**0.6***
Celtis occidentalis	20	9	-0.38	-	-	-
Prunus spinosa	1	5	0.67	-	-	-
Robinia pseudoacacia	1	33	0.94*	-	-	-
Rubus spp.	-	-	-	5	6	0.09
Salix caprea	-	-	-	10	30	0.5
Sambucus nigra	8	10	0.11	-	-	-
Forbs	**29**	**27**	**-0.04**	**2**	**16**	**0.78**
Ballota nigra	0.33	7	0.91	-	-	-
Medicago sativa	5	16	0.52	-	-	-
Grasses	**6**	**8**	**0.14**	**85**	**39**	**-0.37***

diet in 1998, while proportion of alfalfa was only 4% in the diet in 2000. Maize has never been consumed in this period of the year.

Diet diversity, evenness of diet and the number of consumed species were similar between forest and agricultural areas (Table 3).

Table 3. Diet diversity, evenness and number of species in red deer diet in the forest and in the agricultural area. In 1998 values were determined from the faecal samples collected on 15 June, while in 2000 results of three samplings (15 and 30 June, 15 July) were averaged (SD in bracket).

	Forest area		Agricultural area	
	1998	2000	1998	2000
Diversity	2.19	2.02 (0.21)	2.22	2 (2)
Evenness	0.81	0.74 (0.08)	0.92	0.73 (0.12)
Number of species	15	15 (0.6)	11	15 (1.2)

Diet of red deer was similar in nutritive composition between habitat types in 1998, but significantly different in 2000 (χ^2 homogeneity test: df=4, χ^2= 7.23, p>0.05 in 1998; df=4, χ^2=16.41, p<0.005 in 2000). Crude protein content was lower, while crude fibre content was higher in the agricultural area than in the forest in both years (Table 4).

Table 4. Proportion of nutrient contents (g/100 g dry matter) in the forest and agricultural plants and red deer diet in 1998 and 2000. In both years sampling on 15 June was considered for comparison.

Plants/Mixtures	Nutrient contents	Forest area		Agricultural area	
		1998	2000	1998	2000
Celtis occidentalis	Crude protein	23	20.19	-	-
	Crude fibre	11.7	15.72	-	-
Pinus spp.	Crude protein	7.7	-	-	-
	Crude fibre	29.2	-	-	-
Prunus spinosa	Crude protein	20.1	15.14	-	-
	Crude fibre	14.1	13.31	-	-
Robinia pseudoacacia	Crude protein	23.9	22	-	-
	Crude fibre	9.3	17.41	-	-
Sambucus nigra	Crude protein	35.8	29.83	-	-
	Crude fibre	11.5	11.46	-	-
Agropyron repens	Crude protein	-	-	12.83	-
	Crude fibre	-	-	29.2	-
Carex spp.	Crude protein	-	-	9.0	-
	Crude fibre	-	-	27.7	-
Medicago sativa	Crude protein	-	-	24.1	33.68
	Crude fibre	-	-	15.5	16.32
Phragmites communis	Crude protein	-	-	17.1	-
	Crude fibre	-	-	25.5	-
Salix caprea	Crude protein	-	-	13.8	10.25
	Crude fibre	-	-	12	17.48
Triticum aestivum	Crude protein	-	-	17.0	-
	Crude fibre	-	-	25.1	-
Diet mixtures	Crude protein	**25.14**	**23.60**	**13.41**	**17.16**
	Crude fibre	**11.68**	**15.74**	**22.73**	**22.49**
	Crude fat	**2.39**	**4.04**	**2.67**	**3.42**
	Crude ash	**6.45**	**8.44**	**7.56**	**27.13**
	N-free extracts	**54.33**	**48.17**	**53.62**	**29.79**

Discussion

The diet of red deer contained several plant species in both habitats. Intensive foraging on browse even in the agricultural area is in agreement with Hofmann's (1985) definition of red deer as an intermediate feeder. An important role of browse in red deer diet have already been found in earlier studies (Hearney & Jennings 1983, Mátrai & Kabai 1989, Homolka 1990). Although, plasticity in food selection is also manifested by the high proportion of the other forage groups in the diet, such as grasses in the agricultural area. Changes in the diet composition of red deer following phenological stages of vegetation were reported by Chen et al. (1998). Adaptation to varying feeding conditions throughout seasons or years was also confirmed by Groot Bruinderink & Hazebroek (1995). Diet selection of red deer in our study area is agreement with the results.

One of our hypothesis was, that red deer consume predominantly cultivated plants in the agricultural field. However, this is not the case. Cultivated plants were not dominant diet components, their presence in the diet was rather negligible. This fact shows that easy reach of cultivated plants does not manifest in their high consumption, consequently it should not mean significant reason for the seasonal home range shift. Diet diversity, evenness and number of consumed species were similar in both habitats. Intensive feeding on over dominant cultivated plants would cause a significant decrease in the values of these variables. Nevertheless, it seems that feeding behaviour of red deer is rather constant in highly different habitat types; red deer selects for browse species, but its choice among plant species is adjusted to the actual food supplies.

Comparison of diet qualities between habitats could not support our hypothesis on nutritive benefits of agricultural diet. Nutritive composition of the two represented diet differed significantly. But because of the high energy cost and risk of the travel between the two habitats significant benefits were expected in the agricultural field. These differences, however, confirmed the better quality of forest food. High quality food should have high level of crude protein and low level of crude fibre (Chen et al. 1998). Animals are able to select better food according to these two directives (see Dalley et al. 1999, Jacobs et al. 1999 for works on cows). Much lower crude protein and much higher crude fibre contents of agricultural than forest diet therefore, should be disadvantageous for red deer and contradict to the assumption that feeding is one of the reasons for home range shift, as Georgii (1980), Schmidt (1993) and Borkowski & Furubayashi (1998) suggested before. Although actual results could not confirm it, temporal quality changes of available forage during a longer time interval could be a potential cause of a home range shift. If nutritive composition of the diet would become better in the agricultural area or worse in the forest than in the other area after shifting, then red deer could gain advantages by shifting later. Nevertheless, our findings about agricultural diet are very surprising and lead us to apply new approaches for understanding this special ranging behaviour. What could be the main reasons therefore?

Larger feeding patches and so lower travelling time could be favourable in the agricultural area, but avoidance of cultivated plants doubts this theory. Human disturbance could also have effects on this seasonal movement. But there are no intensive forestry works in June, even human disturbance is always much higher in the agricultural area at this time. From another point of view we could hypothesise that social effects among individuals could affect not only home range use of stags (Kammermeyer & Marchinton 1976, Bobek et al. 1987), but that of hinds as well; and so shifting would be the solution to decrease intraspecific competition in the forest. Moreover we could also suppose, that there is no significant difference between the two habitats from the view of red deer. When sufficient food is available in the agricultural area a part of the population shifts to this field, but no meaningful advantage will derive from this ranging strategy. We experienced that these strategies are very stable within individuals over the years and we believe, that calves learn and will follow the strategy of their mother (young stags follow home range pattern of their mother, see Georgii & Schröder 1983). In this way both behavioural variations could be viable and could exist in a relatively stable ratio in a stable red deer population.

Hence comparison of social status, condition, habitat use and preferences of different ranging strategists would help us to reject some hypotheses and decide where to find the reason for this home range shift: in the forest or in the agricultural area? Wildlife management really needs this knowledge because it seems that damages caused by red deer in the forest and agricultural areas could not be decreased considering only one of these habitats. Red deer use entire forest-agriculture complexes and that is why management planning should be conducted both at habitat and landscape-level.

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