

## Density of red and roe deer and their distribution in relation to different habitat characteristics in a floodplain forest

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**Abstract.** Density and distribution of red deer (*Cervus elaphus* L., 1758) and roe deer (*Capreolus capreolus* L., 1758) in relation to habitat structure and distribution of food sources was studied using simple faeces transects and monitoring plots during winter in a floodplain forest along the Morava River. Deer densities detected on monitoring plots and parallel simple faeces transects were comparable, so we used the faeces transects, thus enabling us to gather data from a larger part of study area. Densities of both species were relatively high (red and roe deer; 9.6 and 7.0 ind./km<sup>2</sup> respectively). Red deer preferred forest stands with dense (60–80 %) cover and a diversified shrub layer (more than three tree species). Roe deer mainly used old stands of age 50–99 years with a high cover of canopy layer and conversely low cover of herb layer, dominated by bramble. A positive relationship between the distributions of both species was detected. Inter-specific spatial interference was not observed, despite their high densities in the study area.

**Key words:** abundance, *Capreolus capreolus*, *Cervus elaphus*, habitat selection, woodland

### Introduction

Ungulate species can have an extensive browsing impact on forest vegetation (Kraus 1987, Gill et al. 1996, Motta 1996, Putman & Moore 1998, Gill 2000, Fuller & Gill 2001, Gill & Beardall 2001, Morecroft et al. 2001). Research into deer density and distribution helps in the selection of suitable additional feeding places. It also might be used to protect artificial plantations and naturally regenerating stands against browsing damage (Pađaiga 1998, Homolka & Heroldová 2000) and to assist in rational game management in areas where the abundance of the deer population is controlled by culling (Eberhardt & Van Etten 1956, Bailey & Putman 1981, Marques et al. 2001, Laing et al. 2003).

Deer distribution is influenced by climatic factors (Staines 1976, 1977, Bobek et al. 1984, Latham et al. 1997), habitat structure (König & Gossow 1979), vegetation structure and food supply (Mitchell et al. 1977, Clutton-Brock & Albon 1989). Habitat selection by deer is best viewed as a trade-off between selection of cover and selection of food (Mysterud et al. 1999). The distribution of feeding sources in the forest or near the forest (fields, meadows) can essentially influence deer distribution mainly during winter when the food supply is restricted. Fields with winter cereals or winter rape can offer favourite alternative food sources for deer during winter if they are situated adjacent to the forest (Zejda & Homolka 1980, Putman & Moore 1998). The distribution of deer species can also be affected by inter-specific competition for

food and shelter, e.g. roe deer can be repressed by red, fallow or sika deer (B a t c h e l o r 1960, V l a d y s h e v s k i i 1968, D a n i l k i n 1996, L a t h a m et al. 1996).

High primary production, high biodiversity of the floodplain forest ecosystem (P e n k a et al. 1985) and agricultural fields situated on the western margin of the forest offer very specific conditions, which can significantly influence habitat selection of animal species living there. All these characteristics of habitat reflect surplus and heterogeneity of the food for herbivore species and a high density is expected. Previous studies from the floodplain forest showed that shoots of broadleaved trees play an essential function in the diet of ungulates: roe deer (*Capreolus capreolus* L., 1758) (B a r a n ě k o v á 2004) and red deer (*Cervus elaphus* L., 1758) (P r o k e š o v á 2004). Consequently, their distribution in this habitat can be mainly dependent on the structure and characteristics of the shrub layer. Intensive tree cutting has considerably remodelled the structure of the forest and created a mosaic of several small plots of different age that offer different qualities of food supply and available shelter, which can influence spatial game activity (T o m a & K o l o č á n y 2000).

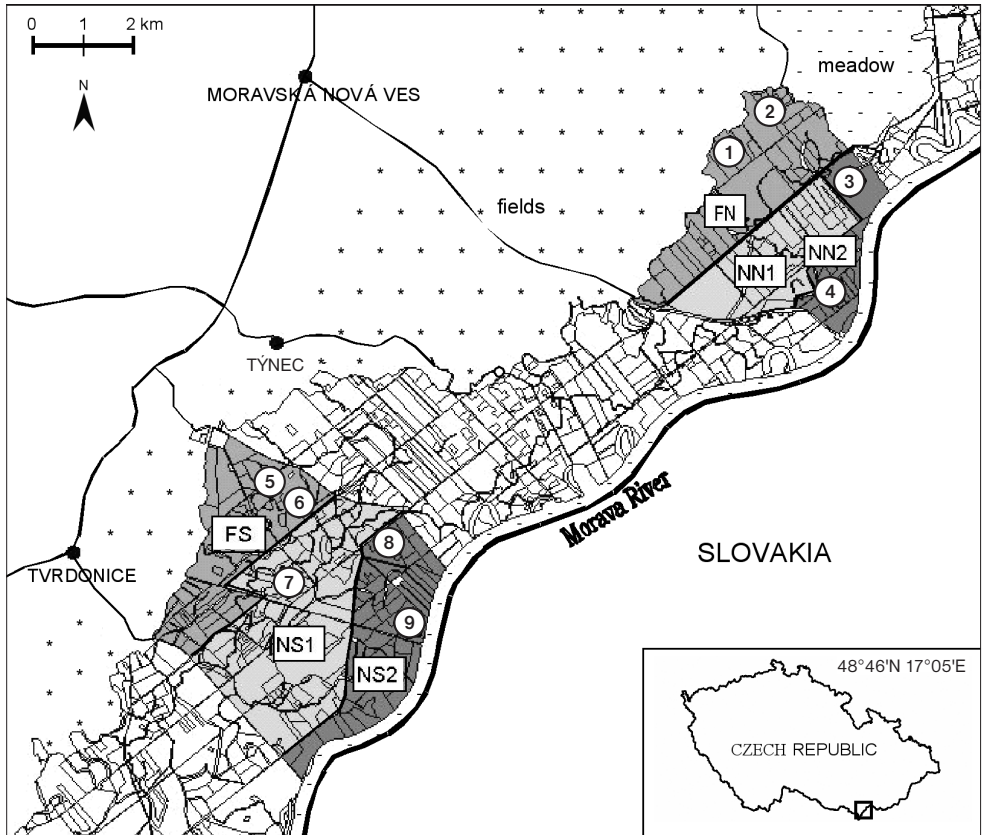
The present study describes the density of red and roe deer in the floodplain forest along the Morava River and examines the relationship between habitat characteristics and deer distribution during winter. We studied the habitat preference of red and roe deer and expected both species to prefer dense shrub layer, but also to gather in habitats near fields that provided suitable food supply after harvest. We also tested the hypothesis of a negative influence of red deer on roe deer due to expected inter-specific spatial interference in the study area.

## Study Area

The study was carried out during three winters 2001/02, 2002/03 and 2003/04 in the floodplain forest along the Morava River in the south-eastern part of the Czech Republic near the border with Slovakia (48°46'N 17°05'E). The study area of 1 041 ha is situated at an altitude of 200–220 m a.s.l. (Fig. 1).

The study area consists of forest (68 %), fields (19.2 %) and meadows (12.8 %). Commercially managed forest (708 ha) is classified as *Querceto-Fraxinetum* and *Ulmeto-Fraxinetum*. The dominant canopy tree species are oak (*Quercus robur*, *Q. petraea*), ash (*Fraxinus excelsior*, *F. angustifolia*) and field maple (*Acer campestre*). Less abundant but regularly occurring are poplar (*Populus* spp.), box elder (*Acer negundo*), elm (*Ulmus laevis*), common alder (*Alnus glutinosa*), black walnut (*Juglans nigra*) and lime (*Tilia* spp.). Shrubby vegetation is well developed and diversified. In addition to the previously mentioned tree species we found blackthorn (*Prunus spinosa*), blood-twig dogwood (*Swida sanguinea*), hawthorn (*Crataegus* spp.), spindle (*Euonymus* sp.), willow (*Salix* spp.), elder (*Sambucus nigra*), and rose (*Rosa* spp.). The shrub layer is formed by artificial plantations of economically important seedlings (mainly ash and oak) and also in many sites by naturally regenerating stands. The herb layer is also well developed in many places of the study area with *Rubus* spp., *Galium* spp., *Urtica dioica* and invasive *Aster novi-belgii* being dominant.

Larger meadows are situated along the eastern (bank of the Morava River) and north-western edge of the forest (the research carried out on the 500 m wide strip); smaller meadows are also found inside the southern part of the forest. The total size of meadows is 133 ha. Fields are situated on the western edge of the forest (maize, rape, winter cereals; Fig. 1). Research was only carried out on a 500 m wide strip of fields around the forest border (200 ha).



**Fig 1.** GIS afforestation map of the study area with 2 sub-areas and with subplots in grey colour scale marked with letters in squares (abbreviations the same as in Table 3). The monitoring plots are marked with numbers from 1 to 9 in the circle. The field area is designated with stars, meadow area with dashes.

The entire study area consisted of two sub-areas: northern and southern. We expected differences in deer distribution between these two sub-areas, because the northern sub-area has large meadows on the north-western edge and the southern sub-area has meadows in the middle of the forest (Fig. 1). Also the northern area is narrower and represents the end of red deer distribution range in the floodplain forest, so the density of red deer was expected to be lower there. Because the density of both deer species was expected to be different in both sub-areas, some differences in selection of both species' habitat were also expected.

Each sub-area was divided into three subplots based on the proximity of potential food resources (grasses or field crops): a subplot at the edge of the forest near fields (FN and FS), a subplot in the central part of the forest (NN1 and NS1) and a subplot at the edge of the forest near meadows along the Morava River (NN2 and NS2) (Fig. 1).

## Material and Methods

The density of both species, red and roe deer, was assessed using two methods: clearance plot method and simple faeces transects. Re-counting of winter pellet groups was made on monitoring plots (clearance plot method) established for purposes of the browsing impact

study (B a r a n ě k o v á et al., in prep.), so they were laid out in optimal habitat for deer with abundant shrub layer. Nine monitoring plots 4 x 50 m in different parts of the study area (Fig. 1) were chosen; four and five plots were situated in the artificial plantations and in the natural forest respectively. Size and number of monitoring plots were established in agreement with methods successfully used in other forest habitats (mixed and coniferous forests) in the Czech Republic (B a r a n ě k o v á et al. 2002), as deer ecology in the floodplain forest has so far been neglected. We tried to confirm among other things their exploitation of this habitat.

The monitoring plots were always cleared in November of each year and in March of the following year the winter pellet groups were counted. Density of species was estimated using the following formula:  $D [ind./km^2] = n * 10^6 / (S * t * f)$ , where  $n$  is the number of winter pellet groups found on the plot,  $S$  is the size of the plot in  $m^2$ ,  $t$  is the time (in days) of plot exposure and  $f$  is the defecation rate of the respective species. We used defecation rates 19 and 14 per day for red and roe deer respectively (D o b í á š et al. 1996). The assessment of deer density on monitoring plots was used for detection of the correct time of exposure, because the same time was used for density estimation using simple faeces transects. Data were also used to assess the relationship between deer density and their browsing impact (B a r a n ě k o v á et al., in prep.).

The second method, the counting of winter pellet groups on transects (simple faeces transects), was used for the estimation of the species density and for detection of the influence of habitat characteristics on deer distribution. These transects were 2m wide and 50 m long and were placed randomly through the study area in stands of different age and tree composition (at least three transects 50m long in each type of forest stand depending on the stand size), making sure that transects did not follow access to deer pathways. Exactly 354 transects of 50m long (i.e. 0.5% of the forest area) were used each year. Pellet groups were included into the count only if more than half of the pellet group was lying on the transect. Deer density was calculated from the number of pellet groups found on monitored transects using the above-mentioned formula (same starting date of the exposure was used as we did not find any faeces in November 2002 and 2003 on monitoring plots). To compare the suitability of both methods, deer density detected on the transects was then compared with the deer density calculated in the monitoring plots. Only transects placed along monitoring plots in the same forest stand were used for this comparison to assure data consistency.

The vegetation structure was also mapped using the line transect method in March 2003. The mapping was done using the afforestation forest map (Fig. 1) for both study sub-areas. Each sub-area consists of large amount of forest stands of different age and structure (different species composition of canopy and shrub layer, different vegetation density). The transect of 2 x 150 m in size was taken as a representative sample of each forest stand and was used for the mapping of the vegetation. Based on the food analyses for both deer species (B a r a n ě k o v á 2004, P r o k e š o v á 2004), mainly the shrub layer and cover of bramble was mapped as they were the most important food sources for deer during winter. All mapped vegetation variables are shown in Table 1. The simple faeces transects were only made in some forest stands.

Additional data on deer distribution was obtained by snow-tracking (frequency of footprints on snow cover) at the beginning of research in the winter 2001/02. The presence or absence of deer footprints was recorded in every 50 m of the transect. The total length of the snow tracks was 26.2 km. Snow-tracking was performed on snow cover approximately

1–2 weeks old and 10 cm deep. During the following two winters the patchy and low snow layer made it impossible to repeat the snow-tracking in this area.

The data set on the vegetation variables was modified using arc-sin transformation to increase the homogeneity of data files (Sokal & Rohlf 1981). Differences in the habitat structure (based on variables in Table 1) between subplots were analysed using ANOVA. Differences in the density of deer species between years and subplots were analysed by the  $\chi^2$ -test and ANOVA with regard to data properties. Data obtained by snow-tracking was also analysed by ANOVA. The relationship between habitat variables and deer density was calculated as the correlation between the density of faeces and individual parameters of vegetation, using Pearson correlation coefficient.

## Results

### Vegetation structure

Vegetation structure of the forest stands differed significantly between subplots of the study area. Differences were found for most of the mapped vegetation variables (Table 1). On the other hand, there were no differences in the cover of the canopy layer, herb layer and cover of bramble between subplots (Table 1).

**Table 1.** Differences in the mapped variables of habitat structure between the subplots expressed by ANOVA. In the columns are average values of variables for each subplot, *n* means number of forest stands according to afforestation map, in which they were measured. (F-subplot near fields, N2-subplot near Morava River, N1-subplots in the centre of the forest, N-subplots in the northern sub-area, S-subplots in the southern sub-area).

Subplots/variables <i>n</i>	FN 27	NN1 40	NN2 11	FS 38	NS1 80	NS2 36	Total 232	ANOVA (df=5)	
								F	p
cover of canopy layer (E3)	53.7	38.8	38.9	51.7	51.3	43.2	47.6	1.284	0.272
cover of shrub layer (E2)	20.0	13.9	25.7	18.4	28.6	19.1	21.8	2.510	0.031
cover of field maple (fm)	6.9	5.8	10.4	5.9	17.3	12.6	11.2	3.200	0.008
cover of oak (oak)	1.9	0.5	7.0	3.0	0.6	2.6	1.7	2.298	0.046
cover of ash (ash)	3.5	1.4	0.7	4.6	5.3	2.0	3.6	2.345	0.042
cover of hawthorn (hwt)	0.6	0.7	0.9	1.6	3.9	1.5	2.1	4.060	0.002
cover of blood-twig dogwood (btd)	2.0	2.3	2.9	0.6	0.4	0.3	1.0	4.875	0.000
cover of herb layer (E1)	48.8	45.5	68.8	57.3	51.4	57.6	52.8	1.183	0.319
cover of bramble (rb)	10.3	5.2	3.5	8.0	7.0	4.4	6.7	1.597	0.162
$\bar{X}$ number (N) of species in shrub layer	3.6	4.5	5.0	3.1	3.5	2.4	3.5	4.196	0.001
index field	1	2	3	1	2	3			
index meadow	1	2	1	1	1	1			

Further, we compared the average values of vegetation variables of individual subplots (Table 1) with the average values of these variables calculated from values obtained only in the stands, where the simple faeces transects were made. Except for the cover of the herb layer, which was higher in stands where the faeces transects were made (Wilcoxon test for E1:  $Z = -2.201$ ,  $p = 0.028$ ), other values of variables did not differ. It is possible to say that the stands in which simple faeces transects were made described very well the habitat characteristics of each subplot. They were representative and the density results obtained from them can be used for the whole subplot.

## Density and distribution of red and roe deer (monitoring plots)

### Red deer

The average density of red deer on the study area using data from nine monitoring plots during both winters 2002/03 and 2003/04 was 19.5 ind./km<sup>2</sup> (Table 2). The average density of red deer in the first winter (30 ind./km<sup>2</sup>) was considerably higher than in the second winter (9.0 ind./km<sup>2</sup>). The decrease of density values for red deer was detected in six of the nine monitoring plots (Table 2).

We detected no differences in the usage by red deer of monitoring plots in artificial plantations and naturally regenerating forest stands ( $\chi^2 = 0.337$ ,  $df = 1$ ,  $p = 0.562$ ). Also their density did not differ between northern and southern sub-areas ( $\chi^2 = 0.023$ ,  $df = 1$ ,  $p = 0.881$ ). On the other hand, we detected that the monitoring plots situated far away from fields were preferred in comparison to plots situated near fields ( $\chi^2 = 5.925$ ,  $df = 1$ ,  $p = 0.015$ ).

**Table 2.** Dung density (individual/km<sup>2</sup>) of red deer (ce) and roe deer (cc) on the monitoring plots in both winters and in winter 2002/2003 (03) and 2003/2004 (04) separately (A – artificial plantations, R – naturally regenerating stands, F – monitoring plots near the fields, N – monitoring plots far away from the fields, S – southern sub-area, N – northern sub-area).

Density/ monitoring plots	cc 03	cc 04	$\chi^2$ df=1	p	ce 03	ce 04	$\chi^2$ df=1	p	cc 03/04	ce 03/04
No. 1 (AFN)	15.9	29.5	4.735	0.029	11.7	5.9	1.911	0.167	22.7	8.8
No. 2 (RFN)	82.9	53.7	6.242	0.012	68.1	17.8	29.454	0.000	68.3	43.0
No. 3 (RNN)	41.5	10.7	18.173	0.000	16.5	0	16.500	0.000	26.1	8.2
No. 4 (ANN)	6.4	2.7	1.504	0.220	28.2	11.9	6.626	0.010	4.5	20.0
No. 5 (RFS1)	15.9	0	15.900	0.000	9.1	7.9	0.085	0.771	8.0	8.5
No. 6 (RFS2)	57.4	2.7	49.785	0.000	21.2	7.9	6.079	0.014	30.0	14.5
No. 7 (ANS1)	0	0	-	-	70.5	9.8	45.884	0.000	0	40.2
No. 8 (RNS)	0	2.7	2.700	0.100	16.4	13.8	0.224	0.636	1.3	15.1
No. 9 (ANS2)	9.6	0	9.600	0.002	28.2	5.9	14.583	0.001	4.8	17.1
Average	25.5	11.3	5.479	0.019	30.0	9.0	11.308	0.001	18.4	19.5

### Roe deer

The average density of roe deer assessed using data from monitoring plots during both winters 2002/03 and 2003/04 was 18.4 ind./km<sup>2</sup> (Table 2). The average density of roe deer in the first winter was significantly higher than in the second winter (25.5 ind./km<sup>2</sup> in 2002/03 x 11.3 ind./km<sup>2</sup> in 2003/04). Roe deer density was higher on five of the nine monitoring plots in the first winter in comparison to the second winter. Only on one plot was the density of roe deer during the first winter lower compared to the density in the second winter. The roe deer density was unchanged between winters on the three remaining plots (Table 2).

The density of roe deer on monitoring plots located in natural shrub layer was found to be higher than their density detected in artificial plantations in both winters ( $\chi^2 = 10.103$ ,  $df = 1$ ,  $p = 0.002$ ). Roe deer were also more common in the northern sub-area than in southern one ( $\chi^2 = 11.870$ ,  $df = 1$ ,  $p = 0.001$ ). The difference in roe deer density between monitoring plots located near fields compared to other plots was not significant ( $\chi^2 = 3.604$ ,  $df = 1$ ,  $p = 0.057$ ).

## Density and distribution of red and roe deer (simple faeces transects)

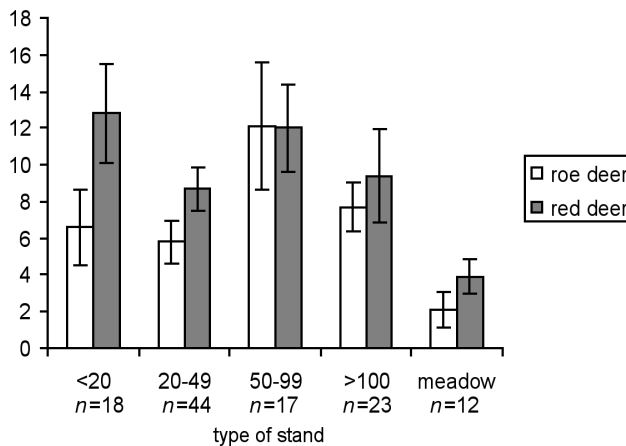
### Red deer

The average density of red deer estimated by counting winter pellet-groups on simple faeces transects during both winters was 9.6 ind./km<sup>2</sup>. The average density of red deer did not differ between winters, 13 ind./km<sup>2</sup> x 8.5 ind./km<sup>2</sup> respectively ( $\chi^2 = 0.942$ ,  $df = 1$ ,  $p = 0.332$ ).

There were no differences between densities of red deer in the subplots (Table 3). Also northern and southern sub-areas did not differ significantly in the density of red deer (ANOVA:  $F = 0.116$ ,  $df = 1$ ,  $p = 0.734$ ). Red deer did not prefer any type of forest stands i.e. artificial plantations and other forest stands of different age (ANOVA:  $F = 1.951$ ,  $df = 4$ ,  $p = 0.107$ ) (Fig. 2). A significantly lower density of red deer was detected on meadows compared to forest habitat (ANOVA:  $F = 4.705$ ,  $df = 1$ ,  $p = 0.032$ ) (Fig. 2).

**Table 3.** Average values of red and roe deer density (individual/km<sup>2</sup>) in winters 2002/3 and 2003/4 and average values for both winters together on the individual subplots (simple dung transects). Differences between subplots are expressed by ANOVA. (Abbreviations of subplots are the same as in Table 1).

Density/subplots	cc 03	cc 04	cc 03/04	ce 03	ce 04	ce 03/04
FN	11.1	24.9	18.4	10.2	10.1	10.2
NN1	11.5	5.1	7.7	15.9	5.5	9.7
NN2	7.0	5.9	6.2	14.4	8.3	9.9
FS	8.4	3.1	4.6	6.9	7.1	7.1
NS1	3.5	3.2	3.3	20.1	11.1	12.9
NS2	6.0	4.1	4.4	9.2	7.3	7.6
F (ANOVA, df=5)	0.720	15.328	9.791	0.992	0.656	1.075
p (n)	0.614(32)	0.001(82)	0.001(114)	0.442(32)	0.658(82)	0.378(114)



**Fig 2.** Average values of the roe and red deer density (individual/km<sup>2</sup>) on forest stands of different age and on meadows (with error bars).

### Roe deer

The average density of roe deer estimated by counting winter pellet-groups on the simple faeces transects during both winters was 7.0 ind./km<sup>2</sup>. The density of roe deer seemed to be stable during both winters, 8.9 ind./km<sup>2</sup> x 6 ind./km<sup>2</sup> respectively ( $\chi^2 = 0.564$ ,  $df = 1$ ,  $p = 0.453$ ).

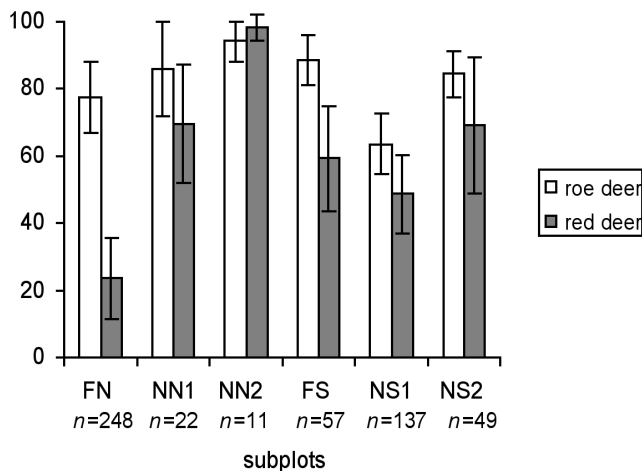


The density of roe deer was similar in all subplots during the first winter. On the other hand, in the second winter the density on the subplot FN was much higher compared to other subplots (ANOVA:  $F = 9.791$ ,  $df = 5$ ,  $p \ll 0.001$ ; following Scheffe post-hoc test) (Table 3). The preference of the FN subplot caused an increase in roe deer density in the northern sub-area in comparison to the southern one,  $11.8$  individual/km<sup>2</sup> x  $4.1$  individual/km<sup>2</sup> respectively (ANOVA:  $F = 21.628$ ,  $df = 1$ ,  $p \ll 0.001$ ).

Roe deer used individual stands of differing age differently (ANOVA:  $F = 2.653$ ,  $df = 4$ ,  $p = 0.037$ ) (Fig. 2). The roe deer density was highest in older stands (age 50 to 99 years); the lowest density was detected on meadows. The different density of roe deer on meadows and forest habitat is on the border of significance (ANOVA:  $F = 3.847$ ,  $df = 1$ ,  $p = 0.052$ ).

### Snow tracking

Footprints of red deer were found on 58% of the 50 m long segments of transects that intersected the study area. We did not find any difference in distribution of red deer footprints on snow cover between six subplots (ANOVA:  $F = 2.172$ ,  $df = 5$ ,  $p = 0.084$ ) (Fig. 3). Also the difference in footprint distribution between the northern and southern sub-areas was not significant (ANOVA:  $F = 0.500$ ,  $df = 1$ ,  $p = 0.484$ ). The frequency of footprints in the subplots situated near fields (FN and FS) was similar to the frequency of footprints in subplots away from fields (ANOVA:  $F = 3.562$ ,  $df = 1$ ,  $p = 0.068$ ) (Fig. 3). Red deer used artificial plantations and natural shrub layer with the same intensity similarly as it was in the case of meadows and forest habitat. Red deer avoided the field habitat (ANOVA:  $F = 8.345$ ,  $df = 2$ ,  $p = 0.001$ ) (Fig. 4).

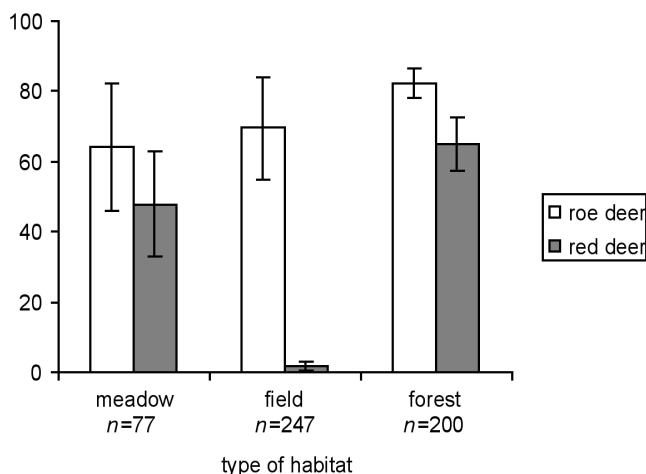


**Fig 3.** Relative frequency (%) of red and roe deer footprints on snow cover in 50 m long sections of the transects intersected subplots of study area (abbreviations same as in Table 2)(with error bars).

Footprints of roe deer were found on 78% of the 50m long sections of transect. Roe deer did not show preference for any of the subplots (ANOVA:  $F = 1.158$ ,  $df = 5$ ,  $p = 0.352$ ) (Fig. 3). Footprint distribution was similar in the northern and southern sub-areas (ANOVA:  $F = 0.798$ ,  $df = 1$ ,  $p = 0.378$ ). A preference for subplots near fields compared to other subplots was not detected (ANOVA:  $F = 0.559$ ,  $df = 1$ ,  $p = 0.460$ ). There was also no difference between roe deer distribution in artificial plantations and in other types of forest



stands. Roe deer footprints were distributed evenly in fields, meadows and in forest habitat (ANOVA:  $F = 1.413$ ,  $df = 2$ ,  $p = 0.258$ ) (Fig. 4).



**Fig 4.** Relative frequency (%) of red and roe deer footprints on snow cover in floodplain forest, on adjacent meadows and fields (with error bars).

#### Relationship between deer distribution and habitat characteristics

The highest density of red deer was found in stands with high cover of shrub layer (60–80 %). A significantly positive correlation was found between the density of this species and the cover of field maple and hawthorn ( $p < 0.01$  and  $p < 0.05$ , respectively) (Table 4). Red deer density was also higher in stands with a diversified shrub layer ( $p < 0.01$ ). Other vegetation variables showed no significant relationship to red deer density.

Roe deer density positively correlated with cover of bramble ( $p < 0.01$ ) and negatively correlated with cover of the herb layer ( $p < 0.01$ ), so it seems that roe deer preferred places with a relatively lower cover of herb layer formed mainly by bramble (Table 4). A significant relationship was also detected between the cover of the canopy layer and roe deer density ( $p < 0.05$ ). Other vegetation variables showed no relationship to roe deer density.

**Table 4.** Positive (+) and negative (-) mutual correlations between vegetation structure variables and red and roe deer density in the floodplain forest (Pearson correlation coefficient ( $r_p$ ); \* $p < 0.05$ ; \*\* $p < 0.01$ ).

Variables/density n=114	E3	E2	fm	oak	ash	btd	ht	E1	rb	N
roe deer	0.209*	-0.032	-0.054	0.109	-0.077	0.064	-0.036	-0.249**	0.350**	-0.038
red deer	0.137	0.335**	0.318**	-0.005	-0.011	0.060	0.197*	-0.119	0.119	0.190*

#### Relationship between distribution of red and roe deer

The analysis of red and roe deer density did not confirm our hypothesis about spatial interference between red and roe deer (Table 5). On the contrary, a positive correlation in density of red and roe deer was found in old forest stands (older than 100 years). In other forest stands and on meadows, no relationship between density of red and roe deer was recorded (Table 5). Red and

roe deer were found cohabiting in the southern sub-area and on the subplots away from fields. No relation between their densities was observed in other parts of the study area.

**Table 5.** Relationship between red and roe deer density in forest stands of different age, on meadows, in different parts of the area and in whole study area (total) of the floodplain forest (Pearson correlation coefficient ( $r_p$ ); \* $p < 0.05$ ; \*\* $p < 0.01$ ).

Correlation n=114	<20	20–59	60–99	>100	meadow	forest	NS	SS	FN+FS	NN+NS	Total
cc x ce	-0.290	0.222	0.262	0.517*	-0.160	0.195*	0.184	0.345*	0.257	0.308**	0.217*

## Discussion

Objective data about deer density are obtained problematically but are essential for deer management and the study of deer impact. To use direct census is very difficult in woodland (Bailey & Putman 1981), so an indirect method of pellet-group counting is preferred for detection of deer density, distribution and habitat preference analyses (Benett et al. 1940, Riney 1957, Neff 1968, Putman 1984). The application of this method is possible because deer seem to defecate evenly in space and time in habitat without using special latrines or using faeces as territory markers (Mitchell et al. 1985). In our study, we counted pellets during spring (March), the best appropriate season for pellet counting because pellet groups build up over winter owing to the much lower decay rate and are not decomposed by invertebrates (Mitchell et al. 1985, Aulak & Babinska-Werka 1990, Welch et al. 1990). Also they can be more easily found in sporadic vegetation (Latham et al. 1996). In the floodplain forest it is almost impossible to find deer pellets during the growing season owing to a dense herb layer and fast decomposition due to invertebrate attacks (own observations).

On the other hand, this method could bias deer density estimation in natural habitats and lead to an inaccurate estimation. The common causes of errors could be uneven distribution of individual deer, habitat preference, differences in mobility of individuals, different defecation rate as a consequence of intra-specific variation, age, type of food and season. Overlooking of some pellet groups on the plots or subjective distinction between old and new pellet groups by researchers can also bias results (Rogers et al. 1958, Neff 1968, Bailey & Putman 1981, Putman 1984, Staines & Ratcliffe 1987, Padiga 1998). All these problems lead to an underestimation of animal density (Van Etten & Benett 1965, Pucek et al. 1975). Appropriate width of the transects (in our study two metres) can reduce errors caused by overlooking pellets if the area is too big (Buckland et al. 1993).

Two methods, the re-counting of winter pellet groups on monitoring plots (clearance plot method) and non-recurring counting of winter pellet groups on simple faeces transects (standing crop method) were used to estimate relative deer density in the present study. The density of both species estimated using monitoring plots was much higher mainly in 2002/03 than by using the simple faeces transect method. This result might reflect a preference for these monitoring plots compared to other parts of the forest. The plots were chosen mainly to study browsing impact, so the shrub layer (cover of broadleaved trees) was of high quality there. Compatibility of results from simple faeces transects and monitoring plots was confirmed by comparison of data from monitoring plots with data from transects located near the plots in the same forest stand. The difference in density estimated by both

of these methods respectively in the same habitat type were not significant for either red deer (19.5 individuals/km<sup>2</sup> x 18.1 individuals/km<sup>2</sup>,  $\chi^2 = 0.052$ ,  $df = 1$ ,  $p = 0.819$ ) or roe deer (18.4 individuals/km<sup>2</sup> x 16.2 individuals/km<sup>2</sup>,  $\chi^2 = 0.140$ ,  $df = 1$ ,  $p = 0.71$ ). So, both methods gave the same results and the time of exposition (time of the faeces accumulation on transect) could be used in both methods.

Due to the high heterogeneity of the studied forest (large number of stands of different habitat structure because of intensive harvesting), the method of simple faeces transects was a more suitable method for density estimation than the method of monitoring plots. Coverage of a larger study area by transects compared to areas of the monitoring plots enabled better density estimates. The faeces transect method is more preferable also in areas with very low deer density which require an analysis of a larger area (Marques et al. 2001). The use of the simple faeces transect method is suitable for the estimation of deer density in the floodplain forest because of a very high decay rate in the growing season. All winter pellet-groups decomposed during the growing period (high abundance of insect decomposers) or their features is dramatically changed so much that it is impossible to count the pellets from the previous winter and the clearing of the plot is unnecessary (Neff 1968, Aulak & Babinská-Werká 1990, Lehmkühlet al. 1994). In different habitat types, winter pellet-groups could easily have accumulated over several winters because of the slow decomposition process (up to 21 years in the case of prefall conifers in North England) (Myle & Peace 1998).

Deer density is limited by food supply and by the carrying capacity of the habitat. For example in the mixed forests of Lithuania, it has been assessed that more than 5 individual deer/km<sup>2</sup> can not be tolerated without a possible negative impact of deer on forestry (Balešic & Bluzma 1999). In beech woods in Germany, Kraus (1987) observed changes in the vegetation structure with consequent benefit of grasses, when deer density reached over 3 ind./km<sup>2</sup>. Our density estimates go significantly over those levels and are higher than in other forest habitats in the Czech Republic (Homolka 1993, Prokešová et al., in prep.), so the substantial impact on shrub vegetation can be expected if the food supply is limited there. But we detected lower browsing impact (the intensity of browsing of broad-leaved trees was 30 %) than in other parts of the Czech Republic (Prokešová et al., in prep.). Also the densities of deer seem to be stable between years without significant decline as a consequence of competition (Latham 1999).

Against the food limitation is also the fact that roe deer were not negatively influenced by red deer. In the areas with limited food supply, the negative influence of red deer on roe deer can be evidence of inter-specific competition (Bachelier 1960, Vladyshevskij 1968, Danilkin 1996, Latham et al. 1996). In the floodplain forest, the densities of both deer species showed mutual positive correlations or there were no relationship between them. Their distribution was generally independent and sometimes they preferred very similar forest stands during winter. Our data did not enable us to find out if they used the same plots simultaneously or in different periods of time. For analysing of intensity of their mutual spatial interference, additional data on dynamics of their distribution during winter are necessary. Our results indicate that food supply is not limited in the floodplain forest and both species can flourish in the same habitat even at high densities.

Our hypothesis about preference of plots near fields by red deer was not confirmed. The distribution of red deer during winter had no relation to the western margin of the forest. The results of snow-tracking showed that footprints of red deer were not present on fields. Based

on the data obtained by simple faeces transects, red deer preferred mainly the parts of the forest which were away from fields, i.e. distant to villages. One of possible reasons for this preference could be human disturbance. Fields were used by red deer only when maize was ripening, which formed a very important part of their diet and also offered suitable shelter at the end of summer (P r o k e š o v á 2004).

Winter rape, a rich food source situated near the subplot FN, was not found to be part of roe deer diet during winter (B a r a n ě k o v á 2004). The high density of roe deer in this subplot might be more related to the abundance of bramble, which seems to be an important part of roe deer diet (B a r a n ě k o v á 2004) due to its high nutritional value (own unpubl. data) than to vicinity of fields. The cover of bramble on subplot FN is the highest in comparison to two other subplots in the northern sub-area – NN1 a NN2 (see Table 1). Bramble is an important food source of roe deer during winter in various parts of Europe (S i u d a et al. 1969, H e a r n e y & J e n n i n g s 1983, H o m o l k a 1991, T i x i e r & D u n c a n 1996). The dependence of roe deer on bramble might also reflect the preference for habitats with high cover of canopy layer where the bramble dominates in the herb layer. Roe deer preferred different forest stands in the floodplain forest compared to, for example Great Britain, where mainly artificial plantations with an incomplete canopy layer (up to 30 years old) were preferred (R a t c l i f f e 1984, C a t t & S t a i n e s 1987, W e l c h et al. 1990, L a t h a m et al. 1996, L a t h a m 1999).

Conversely to the roe deer diet, bramble was not found to be an important part of red deer diet during winter (P r o k e š o v á 2004) and also a relationship between cover of bramble and density of red deer was not observed. Red deer mainly used the habitat with a dense shrub layer and distribution of red deer in this habitat is related to the presence of the broadleaved tree shoots which seem to be the important food source for them during the whole winter in the floodplain forest, as also during the rest of the year (P r o k e š o v á 2004). Moreover, the dense shrub vegetation seems to offer sufficient shelter (B a t c h e l e r 1960, B o b e k et al. 1984). Finally, it is possible that human disturbance played a bigger role in red deer preference of the dense stands compared to browse availability, as has been found in previous studies in USA (Alberta) (T e l f e r 1981).

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