Folia Zool. – 57(3): 283–293 (2008)

White-tailed deer winter feeding strategy in area shared with other deer species

Miloslav HOMOLKA[1], Marta HEROLDOVÁ[1] and Luděk BARTOŠ[2]

[1] *Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic,v.v.i., Květná 8, CZ-603 65 Brno, Czech Republic; e-mail: homolka@ivb.cz*

[2] *Department of Ethology, Institute of Animal Science, P.O.B. 1, CZ-104 01 Praha 10 Uhříněves, Czech Republic*

Received 25 January 2008, Accepted 9 June 2008

Abstract. White-tailed deer were introduced into the Czech Republic about one hundred years ago. Population numbers have remained stable at low density despite almost no harvesting. This differs from other introductions of this species in Europe. We presumed that one of the possible factors preventing expansion of the white-tailed deer population is lack of high-quality food components in an area overpopulated by sympatric roe, fallow and red deer. We analyzed the WTD winter diet and diets of the other deer species to get information on their feeding strategy during a critical period of a year. We focused primarily on conifer needle consumption, a generally accepted indicator of starvation and on bramble leaves as an indicator of high-quality items. We tested the following hypotheses: (1) If the environment has a limited food supply, the poorest competitors of the four deer species will have the highest proportion of conifer needles in the diet ; (2) the deer will overlap in trophic niches and will share limited nutritious resource (bramble). White-tailed, roe, fallow, and red deer diets were investigated by microscopic analysis of plant remains in their faeces. The volume of bramble decreased in the diet of all four deer species from November to March. The content of conifer needles in the diet of white-tailed and roe deer was negatively correlated with bramble and in spring made up 90 % of their diet volume. On the other hand conifer needles in the diet of red and fallow deer occurred only in January with snow cover. Fallow and red deer started the compensation of winter starvation at least one month earlier than both roe and white-tailed deer. A high content of conifers in white-tailed deer diet in the second half of the winter fully support the presumption about low nutritional food supply and its diet. It can lead to a markedly impaired condition for white-tailed and roe deer and negatively affect their condition. The dietary overlap of four sympatric deer species was extensive in winter. All species share a limited good quality food supply (bramble) when food is scarce, suggesting that interspecific competition may occur.

Key words: *Capreolus capreolus*, *Cervus elaphus*, Czech Republic, *Dama dama*, diet analysis, fallow deer, *Odocoileus virginianus,* red deer, roe deer

Introduction

White-tailed deer (WTD), *Odocoileus virginianus*, were introduced into the Dobříš Forest, Central Bohemia, Czech Republic, about one hundred years ago (Anděra & Hanzal 1995). Population numbers (around 250 head) have remained stable for at least the last 30 years and the deer have not tended to spread into other localities. In comparison with the results of other introductions of this species in Europe, e.g., into Finland (Moilanen 1968, Nygrén 1984, Tiainen 1989), it is curious that the Dobříš population has remained so localized despite the continued interest on the part of hunters in increasing its numbers.

One of the possible factors that may negatively affect the development of the WTD population is insufficient food supply, during winter in particular, reflected in poor physical condition and negatively affecting their reproductive potential (Mattfeldt 1984). The WTD is a concentrate selector (Hofmann 1989), its diet being composed primarily of dicot forbs, sprouts of broad-leaved woody plants, seeds and fruits (Harlow et al. 1975, Dusek et al.1989, Thill & Martin 1989, Jenks et al. 1996). In environments offering insufficient food supply, the diet contains stop-gap components, primarily Norway spruce, indicating limited food supply not only for WTD but for other deer species as well (Andersson & Koivisto 1980, Nygrén 1984, Padajga 1984, Wishart 1984). Cederlund et al. (1980) and Prieditis (1984) argue that roe deer (also a concentrate selector, see Hofmann 1989, and the European equivalent of the WTD) avoid consuming spruce needles because of their low digestibility. Indirect evidence for low palatability of spruce needles for white-tailed deer has been shown in data from Anticosti Island (Potvin et al. 2003) and for other deer species in the Czech Republic (Homolka 1998).

The Dobříš Forest is shared by four deer species, i.e., WTD, roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), and fallow deer (*Dama dama*). According to optimal foraging theory, animals should prefer high quality food components, such as forbs and browse, seeds and fruits in their diet (Mitchell et al. 1976, Demment & Van Soest 1985). Trophic opportunists will increase their consumption of grasses, whereas browsers are compelled to consume less valuable food items, often conifer needles, after the supply of high quality food has been exhausted (Pyke et al. 1977, Putman 1996). A high proportion of conifer needles in the diet thus indicates an insufficient supply of high quality food. Exhaustion of high quality food resources can be caused by large herbivore interspecific competition. Birch (1957) and De Boer & Prins (1990) argue that eventual interspecific competition between any two species is only possible where there is clear evidence of habitat overlap, there is overlap in forage consumed by the two species within those shared habitats, and the shared dietary resources are limiting. For the species of large herbivores of the Dobříš Forest these conditions seem to be met. White-tailed, roe, fallow and red deer do overlap in sharing the habitat (Bartoš et al. 2002). Clear evidence for overlap in forage consumed is still missing, however. Thus the aim of this study was to analyze if competition for food resources with other sympatric deer species could exist. To answer the question, we focused primarily on the respected indicator of a negative effect of trophic competition, Norway spruce and Scots pine needle consumption (Andersson & Koivisto 1980, Cederlund et al. 1980, Nygrén 1984, Padajga 1984, Prieditis 1984, Wishart 1984,). Bramble was used as an indicator of good quality food supply and its exhaustion. Bramble is an important element of the autumn and winter deer diet in Europe (Homolka 1996, Gill et al. 1996, Perrins & Overall 2001, Barančeková 2004).

We tested the following hypotheses: (1) If the environment has a limited food supply, the poorest competitors of the four deer species will have the highest proportion of conifer needles in the diet ; (2) the deer will overlap in trophic niches and will share the limited nutritional resource (bramble).

Study Area

The WTD population in the Dobříš Forest inhabits a range of about 100 km^2, mainly consisting of part of the woodland massif covering the Hřebeny Mountains, the maximum elevation of which is 690 m above sea level. The annual mean air temperature is 7–8 °C and the annual total precipitation is 500–600 mm. The annual average period of continuous snow cover in the territory lasts for 40–50 days (Anon. 1961). In the winter of 1997/98, snow cover of up to 20 cm was present for two weeks in January (including the period of collecting samples of faeces).

The investigation took place in the centre of WTD distribution, over an area of approximately 20 km^2. Here, the elevation varied between 380 and 550 m a. s. l. The study area was covered with continuous woodland, containing meadows up to 0.5 km^2 in area in its central part. In its south-east part the study area adjoins arable land.

The woodland consisted predominantly of conifers (87 %), most frequently Norway spruce (*Picea abies*) (52 %) and Scots pine (*Pinus sylvestris*) (28 %). Of broad-leaved trees, oak stands (*Quercus* sp.) made up 7 % and birch (*Betula* sp.) 3 %, the remaining species representing less than 2 %. Stands of up to 20 years of age covered 15 % of the area, and those over 70 years of age occupying 25 % of the area. In the forest stands the shrub layer consisted largely of spruce and pine, with broad-leaved species (birch, oak) occurring sporadically. Raspberry (*Rubus idaeus*) and bramble (*Rubus fruticosus*) shrubs were represented in places and bilberry (*Vaccinium myrtillus*) was common. Supplementary food was not provided regularly in the area.

Material and Methods

White-tailed, roe, fallow, and red deer faecal pellets were collected in November 1997, January 1998 and March 1998. On each sampling occasion, between 15 and 17 faecal samples for each of the four deer species were collected. To be sure whose faeces we were collecting, we first watched the deer from a hide with binoculars until it dropped its dung.

Diet composition of the deer was investigated by microscopic analysis of plant remains in their faeces (Homolka & Heroldová 1992). From the faecal samples collected, one pellet was removed and used to prepare a microscopic slide. The representation of various food components was estimated on the basis of their relative cover in the microscopic field. In evaluating the overall character of the diet, the components were pooled to form primary forage classes: conifer needles (mostly spruce), browse (leaves and shoots of *Rubus* spp., dwarf shrubs and broadleaved trees), grasses (leaves and stems of grasses, sedges and other grass like herb species), forbs (dicotyledonous herbs and ferns), others (seeds and fruits, lignified parts of herbs and items like roots and mosses which occurred in small volume).

Browse is the largest component in the WTD winter diet. The understorey of forest stands was overbrowsed by ungulates, which results in an almost total lack of shrub layer and a distinct browse line on forest trees. Bramble represented the absolute majority of browse. To get information on its supply we assessed the biomass of bramble leaves in plots 1 m^2 in area in stands where the species showed 100 % ground coverage, by destructive sampling. The collected leaves were dried at 60°C to constant weight. Samples were taken during the growing season May to November (15 samples), January (18 samples) and March (26 samples) (Fig. 4).

Statistics

The data were analyzed using a multivariate General Linear Mixed Model (GLMM) with percentage of conifer needles in the diet as the dependent variable. To account for the repeated measures on the same sites across the period of collecting samples, all analyses were performed using mixed model analysis with the ‘Site’ as a random factor, using PROC

MIXED (SAS, version 9.1). The significance of each fixed effect in the mixed GLMM was assessed by the F-test, on sequential dropping of the least significant effect, starting with a full model. Fixed effects were classes (‘Deer species’ – white-tailed, fallow, red and roe deer; ‘Month’– November, January, and March) and continuous variables ‘Browse’, ‘Grasses’, and ’Forbs’ (all expressed as a percentage in the diet).

We performed two tests to examine the hypotheses of conifer needles as the main indicator for estimating the potential for interspecific competition. First, we focused on the difference in percentage of needles in the diet. Fixed effects were ‘Deer species’, ‘Month’ and an interaction between these two factors (‘Deer species’*’Month’). Least-squares means (further referred as ‘adjusted means’) were computed for the class ‘Month’ and differences between classes were tested by t-test. We used a Tukey-Kramer adjustment for multiple comparisons. Second, associations between conifer needle content in the diet and other main diet components (i.e., ‘Browse’, ‘Grasses’, and ’Forbs’) were estimated by fitting a random coefficient model as described by Tao et al. (2002) with fixed effects ‘Browse’, ‘Grasses’, ’Forbs’, and interactions ‘Grasses’*’Forbs’, ‘Browse’*‘Deer species’, ‘Grasses’*‘Deer species’, ’Forbs’*‘Deer species’, ‘Deer species’*’Month’. (All interaction terms were tested, but are not reported unless statistically significant.) With this random coefficient model we calculated predicted conifer needle percentages and plotted them against other main diet components with predicted regression lines for each deer species and correlation coefficients between the predicted conifer needles percentage and fixed effect values.

An overlap niche index $C=2.\ \Sigma x_i\ .\ y_i/\Sigma x_i^2 + \Sigma y_i^2$ of Zaret & Rand (1971) was calculated, where x_i and y_i are the percentage of volume of the food components i in the diet of species x and y respectively. The index C has limit values from zero (no overlap) to 1 (total overlap of the diet niches).

Results

Fig. 1 shows average numbers and proportions of the four deer species over the past five years as spring number estimates and their harvest (Wildlife management statistics, Příbram Regional Office). In contrast to fallow and red deer, in the harvest report, the figures of white-tailed and roe deer reflect sanitary culling and/or traffic accidents rather than regular hunting activity (Mařík 2003, personal communication).

Conifer needle content in the diet was low in November. In January, its consumption increased in all species (Fig. 1, GLMM: Deer species $F_{(3,\ 181)}$=36.92, P<0.001, Month $F_{(2,\ 182)}$=163.60, P<0.001, Month*Deer Species $F_{(6,\ 182)}$=32.19, P<0.001), roe deer reaching the highest percentage. The percentage of conifer needles in the roe deer diet was significantly higher than that of fallow (P<0.001) and red deer (P<0.001). No significant differences among the other deer species were found. In the spring (March) content of the conifer needles further increased in white-tailed and roe deer, while it dropped down to the November values in fallow and red deer (Fig. 1). Whitetails did not differ from roe deer, as fallow deer did not differ from red deer. Both white-tailed and roe deer did differ from fallow and red deer (all comparisons P<0.001).

Associations between percentage of conifer needles in the diet and other main diet components of white-tailed, roe, fallow and red deer were analyzed in the second model (GLMM: Browse $F_{(1,\ 183)}$=316.37, P<0.001, Grasses $F_{(1,\ 184)}$=84.95, P<0.001, Forbs $F_{(1,\ 181)}$=36.97, P<0.001, Grasses*Forbs $F_{(3,\ 183)}$=18.45, P<0.001, Browse*Deer species $F_{(3,\ 182)}$= 6.45, P<0.001, Grasses*Deer species $F_{(3,\ 183)}$=4.74, P<0.01, Forbs*Deer species $F_{(3,\ 182)}$=4.97,

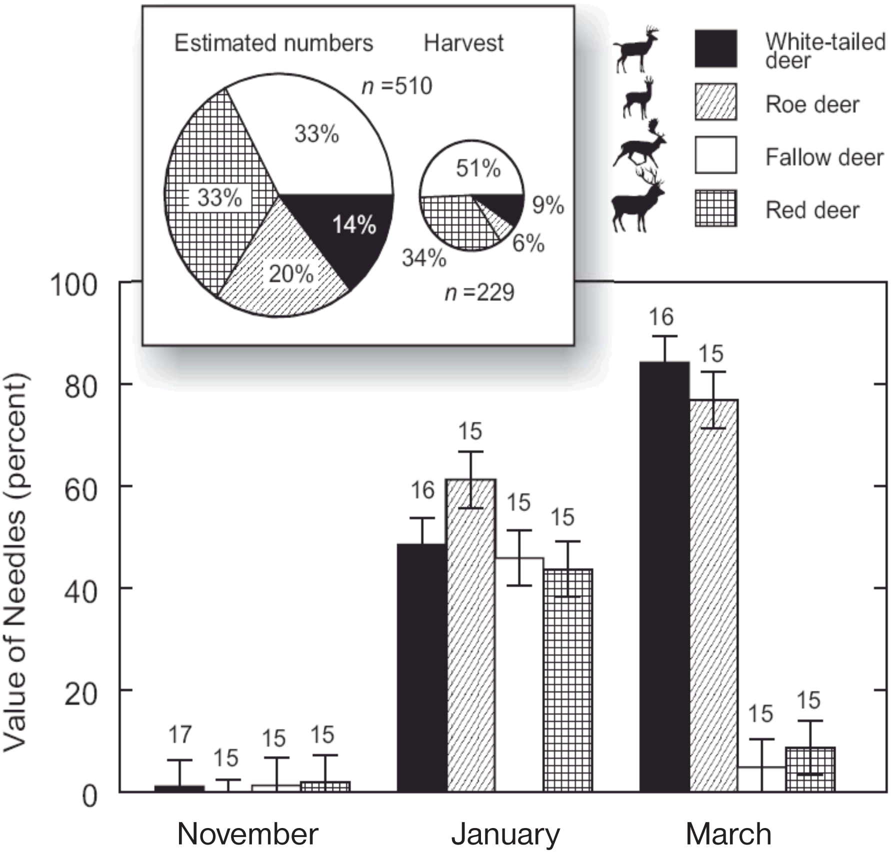

Fig. 1. Adjusted means (± *SE*) of conifer needle percentage in the diet of white-tailed, roe, fallow and red deer in November, January and March (Numbers at end of *SE* = sample size). The inserted part shows the proportion of individual species of the spring deer population estimates (left pie) and proportion of individual species of the deer harvest in the Dobríš Forest, Czech Republic.

$P<0.001$, Month*Deer species $F_{(11, 182)}=20.65$, $P<0.001$). Predicted conifer needle percentages plotted against browse, grasses, and forbs plus correlation coefficients are shown in Fig. 2. a clear reverse association between conifer needles and browse appeared in white-tailed and roe deer but not in fallow and red deer (Fig. 2, top). The increase in conifer needle content in the diet was partly associated with an increase of grass intake in white-tailed and roe but with a decrease of grass intake in fallow and red deer (Fig. 2, middle). There was a significant association between conifer needles and forbs content in white-tailed and roe deer, but not between red and fallow deer (Fig. 2, bottom).

The diet of WTD overlapped mostly with that of the roe deer (a similar trophic specialist) throughout the whole winter season (overlap niche index $C>0.90$), the overlap being greatest at the end of the period (March), when the food supply was reduced to a minimum (Fig. 3, top). The highest general overlap among the species was found in January, the time of permanent snow cover. Because we knew that this was the time of the highest conifer needle intake in all deer species (Fig. 1), we calculated also the index of overlap without the conifer needles to get a better picture of the competition for food resources (Fig. 3, bottom). While the overlap between white-tailed and roe deer was maintained, the similarity of the diets of

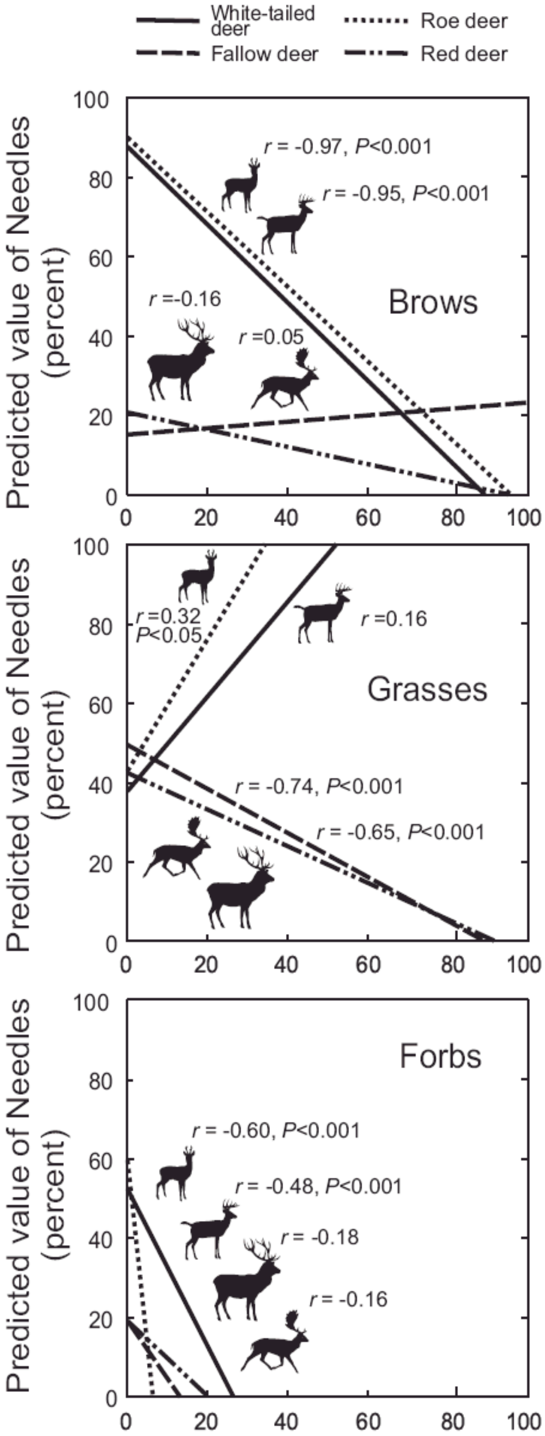

Fig. 2. Predicted conifer needle percentages plotted against browse (top), grasses (middle) and forbs (bottom) for white-tailed, roe, fallow and red deer in the Dobříš Forest, Czech Republic.

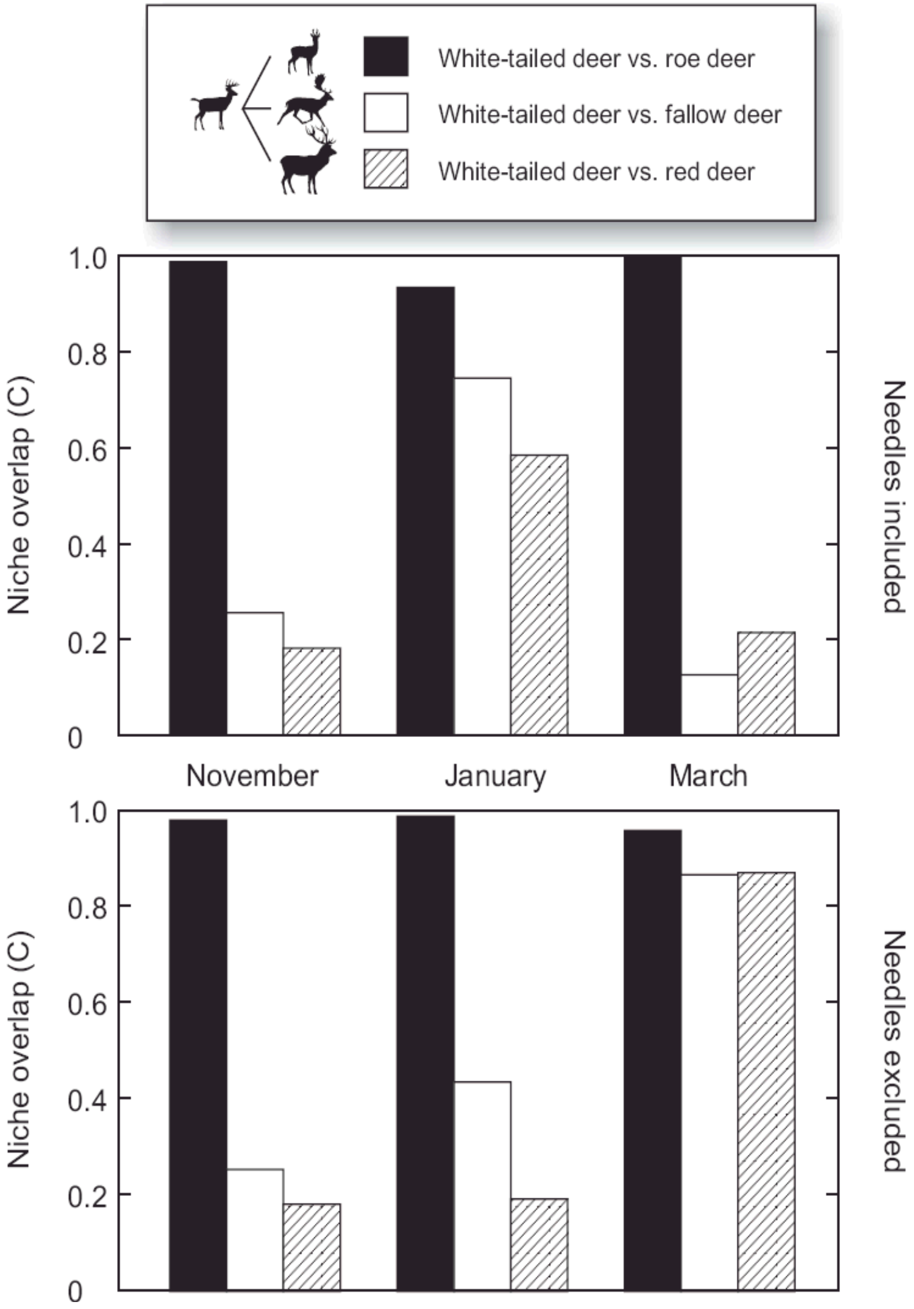

Fig. 3. Overlap of the trophic niches (index *C* after Zaret & Rand 1971) between white-tailed and roe deer, between white-tailed and fallow deer and between white-tailed and fallow deer in November, January and March in the Dobříš Forest, Czech Republic. Indexes included conifer needles in the top figure, while conifer needles were excluded in the bottom figure.

white-tailed and red and fallow deer (trophic opportunists) was low in November, increased in January and reached more than 80% in March.

The resource of browse, generally the most important component of WTD and roe deer diet in winter, was limited in the Dobříš Forest. The biomass of bramble leaves dropped to a minimum in March (Fig. 4) and the volume of browse was under 5% in diets of all deer species.

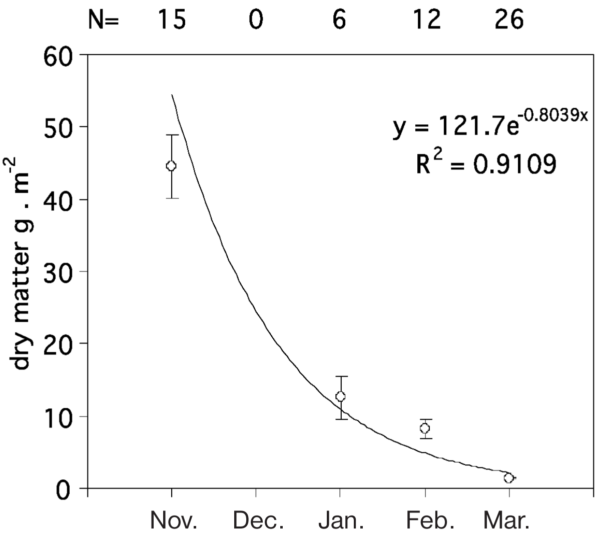

Fig. 4. Gradual exhaustion of bramble food supply indicating depletion of high-quality food items in the Dobříš study area during winter.

Discussion

Our preliminary results fully supported the hypotheses outlined in the introduction concerning the potential competition between white-tailed, roe, fallow and red deer. A rather high proportion of conifer needles occurred in the diet, in white-tailed and roe deer in particular, and an overlap in trophic niches among all species was evident especially in the spring. The most important winter food resource for white-tailed deer (bramble) was exhausted by the middle of winter and all four deer species participated in it. Taking into consideration the numbers of the particular deer species, their daily food consumption, and the percentage volume of bramble leaves in their diets, it appeared that the WTD and roe deer together utilized 33 % in November and 28 % in January of the bramble leaf biomass which was taken by deer. The remaining portion of bramble leaves was depleted by fallow and red deer.

Conifer needles were equally not an important dietary item for any of the species in November. In January, the time of permanent snow cover, its consumption increased in all species. Because of snow cover in January, an increase in conifer needle consumption by all deer species during that period (Fig. 1) need not mean inaccessibility of food resources per se during that time only. The animals could be saving energy instead of searching for more suitable food sources. This is suggested by the fact that the roe deer had the highest conifer needles consumption of all species in January. Being the smallest species, energy cost to move and/or reach food in snow might be also highest for the roe deer. Judging from the browsing frequency, Andersson & Koivisto (1980) have reported that conifer needles form 50–80 % of the WTD diet in Finland in periods of deep snow cover.

Once the snow disappeared (March data), fallow and red deer almost stopped eating conifer needles, while white-tailed and roe deer increased their consumption to 80% or more of the food intake. The high volume of needles in the diet suggests, therefore, a lack of a better quality food supply in late winter. At this time, the trophic overlap (with the conifer needles removed) between all the species was nearly 90% (Fig 3, bottom). Fallow and red deer were apparently utilizing these resources significantly more efficiently than did white-tailed and roe deer. Fallow and red deer started the compensation of winter starvation at least one month earlier than both roe and white-tailed deer. This was because fallow and red deer consumed predominantly grasses, which the white-tailed and roe deer could not utilize these to such an extent. This resulted in WTD being visually in evidently poorer condition than red and fallow deer (LB unpublished data, no record on roe deer available).

The relation of dominant diet items represented in the diets of individual species corresponded with the feeding specialization as determined by Hofmann (1989) and their different diet selection from a nutritional view (Hanley 1997). In roe deer and WTD, a decrease in browse was mostly compensated by conifer needle consumption (Fig. 2). On the other side, red and fallow deer consumption of conifer needles was not associated with the diet supply of browse and its volume in winter diet was not as high as in roe deer and WTD. White tailed and roe deer also substituted the shortage of forbs by an increased consumption of conifer needles. No such response was found for fallow and red deer.

Such trophic conditions can lead to a markedly impaired condition of the animals and may also negatively affect their reproduction (Hesselton & Sauer 1973, Stoll & Parker 1986) and health (De Jong et al. 2004). De Boer & Prins' (1990) conditions for potential interspecific competition have been fulfilled. Also, our data meet Wiens' (1989) criteria for establishing the actuality of competitive interaction. Two species, white-tailed and roe deer, were negatively affected and observed patterns (of population trend or shifts in resource use between sympatry and allopatry) were consistent with predictions from competition. In contrast, fallow and red deer seem to cope with the co-existing species quite well (comp. Henke et al. 1988, Harmel 1997). They maintain their numbers despite being heavily harvested.

As expected, the closest competitor to whitetails was apparently roe deer (comp. Hofmann 1989). In fact, roe deer seems to be the poorest competitor of all four species. Though roe deer had an identical diet niche to white-tailed deer, its occurrence was limited to the edges of the forest complex and its abundance was low, compared to red and especially fallow deer. Thus, even though the white-tailed deer is not prospering well, most likely this exotic has a significant impact on replacing the local roe deer from a substantial part of the area, being its most important competitor. Although the roe deer is the most numerous cervid in Europe (Linnell et al. 1998), interspecific competition with the other larger species such as red and fallow deer has already been suggested (Carne 1954, Delap 1955, Latham et al. 1999; Latham 1999).

In its native environment, the white-tailed deer is well adapted to overcome scarcity of food in the winter season (Verme & Ullrey 1984), if provided with sufficient quality of food in fall to accumulate fat reserves. WTD have been in the area since they were introduced and have been stable for at least 30 years. It may reflect a good ability of the species to compensate for seasonal shortage in food in time of food abundance (Asleson et al. 1997, Grasman & Hellgren 1993). In this WTD may differ from roe deer. Therefore, further research of the Dobříš Forest whitetails taking into account the rest of the season and repeatability of the results obtained is needed.

Acknowledgments

This study was supported by the National Science Foundation´s US-Czech Science Technology Program No. 95036 and by the Grant agency of the Czech Republic No. 206-97-0172. We are indebted to H. Norberg and S. Kankaanpää for providing us with information on Finnish white-tailed deer and translating the most important parts of the articles written in Finnish. The authors would also like to thank R. Putman for his comments on earlier draft of the manuscript and to Ch. C. Mason for final correction of English grammar.

LITERATURE

Anděra M. & Hanzal V. 1995: Atlas rozšíření savců v České republice – předběžná verze.I. Sudokopytníci (Artiodactyla), zajíci (Lagomorpha) (Atlas of the mammals of the Czech Repulic – A provision version. I. Even-toed Ungulates (Artiodactyla), Lagomorphs (Lagomorpha)). *Národní muzeum, Praha (in Czech with English summary).*

Andersson E. & Koivisto I. 1980: Valkohäntäpeuran talviravinto ja vuorokausrytmi (White-tailed deer´s winter food and diurnal rhythm). *Suomen Riista 7: 84–92 (in Finnish with English summary).*

Anonymus 1961: Podnebí ČSSR. Tabulky [Climate of the ČSSR. Tables]. *Hydrometeorologický ústav, Praha (in Czech).*

Asleson M.A., Hellgren E.C. & Varner L.W. 1997: Effects of seasonal protein restriction on antlerogenesis and body mass in adult male white-tailed deer. *J. Wildl. Manage. 61: 1098–1107.*

Barančeková M. 2004: The roe deer diet: is floodplain forest optimal habitat? *Folia Zool. 53: 285–292.*

Bartoš L., Vaňková D., Miller K.V. & Šiler J. 2002: Interspecific competition between white-tailed, fallow, red and roe deer. *J. Wildl. Manage. 66: 522–527.*

Birch L.C. 1957: The meanings of competition. *Am. Nat. 91: 5–18.*

Carne P.H. 1954: Roe deer, fallow and sika. *Oryx 2: 388–391.*

Cederlund G., Ljunquist H., Markgren G. & Stalfelt F. 1980: Food of moose and roe deer at Grimso in Central Sweden – results of rumen content analyses. *Viltrevy 11: 171–247.*

De Boer W.F. & Prins H.H.T. 1990: Large herbivores that strive mightily but eat and drink as friends. *Oecologia 82: 264–274.*

De Jong C.B., Van Wieren S.E., Gill R.M.A. & Munro R. 2004: Relationship between diet and liver carcinomas in roe deer in Kielder Forest and Galloway Forest. *Vet. Rec. 155: 197–200.*

Delap P. 1955: Roe deer and fallow. *Oryx 3: 38–39.*

Demment M.V. & Van Soest P.J. 1985: A nutritional explanation for body-size patterns of ruminants and non-ruminants herbivores. *Am. Nat. 125: 641–675.*

Dusek G.L., Mackie R.J., Herringes J.D. & Compton B.B. 1989: Population ecology of white-tailed deer along the lower Yellowstone river. *Wildl. Monogr. 104: 1–66.*

Gill R.M.A., Johnson, A.L., Francis A., Hiscocks K. & Peace A.J. 1996: Changes in roe deer (*Capreolus capreolus* L.) population density in response to forest habitat succession. *For. Ecol. Manage. 88: 31–41.*

Grasman B.T. & Hellgren E.C. 1993: Phosphorus nutrition in white-tailed deer – nutrient balance, physiological responses, and antler growth. *Ecology 74: 2279–2296.*

Hanley T.A. 1997: A nutritional view of understanding and complexity in the problem of diet selection by deer (Cervidae). *Oikos 79: 209–218.*

Harlow R.F., Crawford J.B. & Skeen J. E. 1975: Deer foods during years of oak mast abundance and scarcity. *J. Wildl. Manage. 39: 330–336.*

Harmel D.E. 1997: The influence of fallow deer and Adouad sheep on white-tailed deer reproduction and survival. *Final report – Federel Aid Grant No. W-127-R-5 Texas Park and Wildlife Department, Austin, Texas: 1–37.*

Henke S.E., Demarais S. & Pfister J.A. 1988: Digestive capacity and diets of white-tailed deer and exotic ruminants. *J Wildl. Manage. 52: 595–598.*

Hesselton W.T. & Sauer P.R.1973: Comparative physical condition of four deer herds in New York according to several indices. *New York Fish and Game Journal 20: 77–107.*

Hofmann R.R. 1989: Evolutionary steps of ecophysiological adaptation and diversification of ruminant: a comparative view of their digestive system. *Oecologia 78: 443–457.*

Homolka M. 1996: Foraging strategy of large herbivores in forest habitats. *Folia Zool. 45: 127–136.*

Homolka M. 1998: Moose (*Alces alces*) in the Czech Republic: chances for survival in the man-made landscape. *Folia Zool. Monographs 1: 1–46.*

Homolka M. & Heroldová M. 1992: Similarity of the results of stomach and faecal contents analyses in studies of the ungulate diet. *Folia Zool. 41: 193–208.*

Jenks J.A., Leslie D.M., Lochmiller R.L., Melchiors M.A. & McCollum F.T. III. 1996: Competition in sympatric white-tailed deer and cattle populations in southern pine forest of Oklahoma and Arcansas, USA. *Acta Theriol. 41: 287–306.*

Latham J. 1999: Interspecific interactions of ungulates in European forests: an overview. *For. Ecol. Manage. 120: 13–21.*

Latham J., Staines B.W. & Gorman M.L. 1999: Comparative feeding ecology of red (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) in Scottish plantation forests. *J. Zool. 247: 409–418.*

Linnell J.D.C., Duncan P. & Andersen R. 1998: The European roe deer: A portrait of a successful species. In: Andersen R., Duncan P. & Linnell J.D.C. (eds), European Roe Deer: the Biology of Success. *Scandinavian University Press, Oslo, Norway: 11–22.*

Mattfeldt G.F. 1984: Eastern hardwood and spruce-fir forest. In: Halls L.K. (ed.), White-tailed deer: Ecology and management. *Stackpole Books, Harrisburg: 305–330.*

Mitchell B., McCowan D. & Nicholson I.A.1976: Annual cycles of body weight and condition in Scottish red deer (*Cervus elaphus*). *J. Zool. 180: 107–127.*

Moilanen P. 1968: Valkohäntäpeuran leviämisestä ja kannan suuruudesta Kanta-Hämeen alueella (On the spread and population size of white-tailed deer (*Odocoileus virginianus*) in Kanta-Häme, Southern Finland). *Suomen Riista 20:37–42 (in Finnish with English summary).*

Nygrén F.A. 1984: Finland. In: Halls L.K. (ed.), White-tailed deer: Ecology and management. *Stackpole Books, Harrisburg: 561–570.*

Padajga V.I. 1984: [Ecological principles of the management of deer populations in Luthuania]. *Dissertation, University of Tartu, Latvia (in Russian).*

Potvin F., Beaupre P. & Laprise G. 2003: The eradication of balsam fir stands by white-tailed deer on Anticosti Island, Quebec: A 150-year process. *Ecoscience 10: 487–495.*

Perrins C.M. & Overall R. 2001: Effect of increasing numbers of deer on bird populations in Wytham Woods, central England. *Forestry 74: 299–309.*

Prieditis A. 1984: Influence of dry food and needles on body weight and consumption of food substances in roe deer, *Capreolus capreolus* L. *Acta Zool. Fennica 171: 213–215.*

Putman R.J. 1996: Competition and resource partitioning in temperate ungulate assemblies. *Chapman and Hall, London.*

Pyke G.H., Pulliam H.R. & Charnov E.L. 1977: Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology 52: 137–154.*

Stoll R.J. & Parker W.P. 1986: Reproductive performance and condition of white-tailed deer in Ohio. *Ohio Journal of Science 86: 164–168.*

Tao J., Littellittle R., Patetta M., Truxillo C. & Wolfinger R. 2002: Mixed Model Analyses Using the SAS System Course Notes. *SAS Institute Inc., Carry, NC, USA.*

Thill R.E. & Martin A. 1989: Deer and cattle diet on heavily grazed pine-bluestem range. *J. Wildl. Manage. 53: 540–548.*

Tiainen J. 1998: Miten valkohäntäpeuran ja metsäkauriin runsauden seuranta tulisi järjestää? (Organisation of small cervid monitoring in Finland). *Suomen Riista 44: 37–42 (in Finnish with English summary).*

Verme J.L. & Ullrey D.E.1984: Physiology and nutrition. In: Halls L.K. (ed.), White-tailed deer: Ecology and management. *Stackpole Books, Harrisburg: 91–118.*

Wiens J.A. 1989: The ecology of bird communities. Volume 2: Processes and variations. *Cambridge University Press, Cambridge.*

Wishart W.D. 1984: Western Canada. In: Halls L.K. (ed.), White-tailed deer: Ecology and management. *Stackpole Books, Harrisburg: 475–486.*

Zaret T.M. & Rand A.S. 1971: Competition in trophical stream fishes: Support for the competitive exclusion principle. *Ecology 52: 336–342.*