

Seasonal composition and quality of red deer *Cervus elaphus* diets in northeastern China

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Seasonal composition and quality of diets of red deer *Cervus elaphus* Linnaeus, 1758 were investigated, basing on microhistological analysis of composite fecal samples in the Less Xingan Mountains, northeastern China. Red deer consumed more graminoids (46%) in spring, shifted to forbs (45%) in summer, and returned to graminoids (35%) in autumn. Availability and high quality [high level of crude protein (CP), and low level of neutral detergent fiber (NDF) and acid detergent fiber (ADF) in forbs in summer] appeared to be two key factors causing these changes in diets. Winter diets were dominated by browses (74%) and the horsetails *Equisetum hiemale* (21%). Three forbs (*Oxalis corniculata*, *Caltha palustris*, *Agrimonia pilosa*) were prevalent in diets during snow-free seasons, and aspen (*Populus* spp.) was an important browse species in all seasons, especially in winter (32%). Forage and diet quality changed seasonally. Dietary CP and *in vitro* dry matter digestibility (IVDMD) declined significantly from spring to winter (from 19.6 to 6.4% and from 61.1 to 32.9%, respectively). In contrast, dietary NDF and ADF increased from 55.6 to 69.9% and from 27.9 to 54.3%, respectively. Red deer diets showed different patterns of seasonal variation in mineral contents. In most cases, dietary Ca, P and K were adequate, but Na appeared deficient all the year round. It is concluded that red deer in this region are typical mixed feeders and their diet shows seasonal changes in quality, similar to those of North American wapiti. Although red deer may have enough protein in most seasons, energy might be a key limiting factor in severe winters.

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Introduction

Intermediate forms between European red deer and North American wapiti occur across Asia (Clutton-Brock *et al.* 1982). *Cervus elaphus* Linnaeus, 1758 is widely distributed from central to northern China and eight subspecies are identified in the whole country (Sheng and Ohtaishi 1993). The subspecies *C. e. xanthopygus* (Mine-Edwards, 1867) from northeastern China is extremely close to the larger phenotype, North American wapiti *C. e. canadensis* in morphology and behaviour (Geist 1987, Ohtaishi and Gao 1990). Although the populations of *Cervus*

elaphus was estimated at 100 000 to 200 000 throughout the country (Sheng and Ohtaishi 1993), it was listed as a second ranked protected species (Ohtaishi and Gao 1990, Sheng 1992) since its populations have been declining as a result of illegal hunting and losses of suitable habitats caused by human activities.

Body size, rumino-reticular volume, mouth size, and incisor breadth impose important constraints on diet selection in wild ruminants (Hanely 1982, Demment and Van Soest 1985, Baker and Hobbs 1987, Hofmann 1989, Illius and Gordon 1987, 1990). Because the ratio of nutrient requirements to gut capacity scales with a negative allometric exponent, it has been argued that large-sized ruminants have relatively low mass-specific energy requirements and thus are adapted to feed on less energy-dense and low quality food items (Bell 1970, 1971, Jarman 1974, Gordon and Illius 1996). Red deer has been classified as an intermediate or mixed feeder (Hofmann and Stewart 1972, Hofmann 1989) and was thought to be an opportunistic feeder that is highly variable and flexible in seasonal diet selection (Hofmann 1989). Results from the extensive studies on composition and quality of diets in European red deer (Gębczyńska 1980, Jamrozy 1980, Clutton-Brock and Albon 1989, Matrai and Kabai 1989) and North American wapiti (Hobbs *et al.* 1981, Baker and Hobbs 1982, Nelson and Leege 1982, Rowland *et al.* 1983, Leslie *et al.* 1984, Morgantini and Hudson 1989, Jenkins and Starkey 1993, Merrill 1994, Gogan and Barrett 1995, Merrill *et al.* 1995) tend to support this. More recently, Merrill (1994) emphasized that seasonal change in availability of forbs may be crucial to changes of food items in wapiti diets. Although a few studies have been reported on food habits of red deer in China (Chen and Xiao 1989, Li and Yan 1989, Li *et al.* 1992, Chen *et al.* 1993), much remains unknown on seasonal composition and quality of diets. Despite wide regional variation that exists in diet composition, it is still expected that red deer in our study area may have similar pattern of diet selection predicted by Hofmann's theory and diet quality similar to that of European red deer and North American wapiti. The purpose of present study was to evaluate these two predictions.

Study area

The study was conducted at Tonghe Hunting Farm, which is situated on the southern slope of the Less Xingan Mountains (45°43'N, 128°40'E), northeastern China and occupies 30 000 ha. Tonghe is a low mountain area with an average elevation of 600 m. The weather is continental and characterized by long, cold winters, and short, hot summers. The annual average temperature is 2.4°C, and extreme temperatures range from about -40.4°C to 36.7°C. The accumulated temperature above 10°C is 2200–2500°C. The average annual precipitation is about 560–700 mm. The frost-free period is 100–105 days, from late April to late September. Snow accumulates in late November, and persists until end of April, and the average snow depth is 43 cm.

Typical vegetation is coniferous-deciduous and deciduous forest. The investigation conducted in winter of 1991, using the point-quarter sampling method (Goldsmith and Harrison 1976), showed that major trees were *Fraxinus mandshurica* (17.3% of relative density), *Pinus koraiensis* (15.1%), *Tilia amurensis* (15.1%), *Phellodendron amurense* (8.5%), *Ulmus* spp. (5.9%), and *Acer mono* (3.7%)

(H. Chen *et al.*, unpubl.). Understorey shrubs mainly include *Corylus mandshurica*, *Deutzia* spp., *Lonicera* spp., *Syringa amurensis*, and *Acanthopanax senticosus*. Common herbaceous layer plants in forests are *Carex* spp., *Urtica* spp. and *Aegopodium alpestre*.

Material and methods

Diet composition

Diet composition was determined by identification of plant cuticular fragments in composite fecal samples. In mid-May 1991, a total of 14 permanent sampling strips (500 × 4 m) oriented east-west were established across 5 feeding sites for collecting fresh pellet groups during snow-free seasons. In October 1991 additional 10 strips were set up. Parallel strips were distributed at least 500 m from one another. Examination of each strip was completed by 2 persons each month and feces were collected until October 1992. In winter, pellet groups were collected following fresh tracks. Pellet groups collected each month from June 1991 to October 1992 were pooled in 4 composite seasonal samples (one pellet from each pellet group), namely spring (45 pellet groups, May), summer (91 pellet groups, June–August), autumn (152 pellet groups, September–October) and winter (570 pellet groups, November–April). Composites were demonstrated to be representative of individual samples in the study of deer nutritional ecology and save much in time and costs despite loss of sample variability (Jenks *et al.* 1989). About 125 plant species were collected from feeding habitats and 2 sets of reference slides were prepared according to Storr (1961) and using the same procedure as fecal slides, respectively.

Fecal samples were oven-dried at 70°C for 24 hr and thoroughly ground. Ground materials were screened through a 0.15 mm sieve to eliminate tiny fragments that were usually unidentifiable. Samples from spring, summer and autumn, and winter were treated by mixed solution of 10% chromic acid and 10% nitric acid (1:1), and concentrated nitric acid, respectively, according to the procedure described by Anthony and Smith (1974), Chen and Xiao (1989), and Gao *et al.* (1991). Thirty slides were prepared from each composite sample and 20 fields of each slide were examined at 100 following Sparks and Malechek (1968). Results were expressed by the relative density of fragments of each food item in each microscopic field, converted from frequency of each food item (Fracker and Brischle 1944).

Forage and diet quality

Forages (food samples) were collected in July, September, November, January, March, and May from 1991 to 1992, at the same 5 feeding sites as those for diet composition. Sedges, forbs, and ferns were collected by simulating the foraging manner of red deer, from at least 10 different plants at each site. Current annual growth of 14 browse species was collected from at least 20 plants at 5 sites. Samples were oven-dried at 70°C for 48 hr and ground through a 0.5-mm mesh in a plant mill. Five composite samples (one sample for each of 5 sites) of sedges, forbs, and ferns for each sampling period were made, respectively, by combining equal amount of ground plant materials of each species. For sedges, forbs and ferns, 4, 8 and 4 species were included, respectively, which were *Carex callitrichos*, *C. campylorhina*, *C. lanceolata*, and *C. siderosticta* (sedges), *Oxalis corniculata*, *Caltha palustris*, *Agrimonia pilosa*, *Anemon raddeana*, *Veronica sibirica*, *Vicia cracca*, *Cacalia hastata*, and *Maianthemum bifolium* (forbs), *Pteridium aquilinum*, *Adiantum pedatum*, *Athyrium acrostichoides*, and *Dryopteris crassirhizoma* (ferns). Duplicate subsamples were analyzed for crude protein (CP) by the macro-Kjeldahl technique (Cullison 1982); neutral detergent fiber (NDF) and acid detergent fiber (ADF) according to Goering and Van Soest (1970); calcium (Ca), sodium (Na) and potassium (K) by atomic absorption spectrophotometry; and phosphorus (P) by spectrophotometry.

In vitro dry matter digestibility (IVDMD) was determined by 2-stage technique of *in vitro* trial following Pearson (1970), but it was modified by using 50 ml centrifuge tubes, each containing a 0.3 g

subsamples and a 30 ml mixture of buffer solution and rumen liquid (4:1). Rumen inoculum was obtained from one red deer captured from its natural habitat in November 1993. The interval from killing the animal to conducting the digestion trial was < 30 minutes. Forages were measured in duplicate and 5 blanks were used in the trial.

We estimated diet quality following Urness *et al.* (1975). For each nutrient, the percent a plant species contributed to the seasonal diets was multiplied by its chemical concentration to yield a weighted nutritional value, and then the nutrient content of seasonal diets was estimated by dividing the summed weighted nutritional values across species by the percent of the total diet accounted for the species analyzed that season. For winter diets, average nutrient values from three sampling periods (November, January and March) were used in the calculation of diet quality.

The other method to estimate diet quality was to include all forage items occurring in the feces in the calculation and the value of the specific nutrient was obtained by summing up the nutrient content of each forage weighted by its proportion in the feces. This method was used by Leslie *et al.* (1984), Jenkins and Starkey (1993), and Merrill *et al.* (1995) in the comparative analysis for the diet quality. Based on the simulated samples produced from the data of diet composition and nutrient contents of forages in this study and Leslie *et al.* (1984), we compared the estimates of the diet nutritional quality using above two methods, and found that results from two methods were very close and no significant difference existed between two methods when the percent of total diet accounted for the forages analyzed was over 60% like this study (67–81%). Thus, we believed that the errors from the different manner of calculating diet quality could be ignored in the comparative analysis.

Statistical analysis

Differences among seasonal diet composition were tested using χ^2 -test. When the null hypothesis was rejected, Bonferroni simultaneous confidence intervals were further established to indicate differences among forage classes (Byers *et al.* 1984). A Spearman rank correlation coefficient (r_s) (Steel and Torrie 1980) was used to examine seasonal trends in diet quality. We compared diet composition and quality of red deer in our region with those of North American wapiti because we required that diet composition data come only from the fecal analysis in all comparable studies and no such data were available from European red deer, using a principal component analysis (SAS 6.0 1989). In the comparison, forages were divided into graminoids (grasses and sedges), forbs, and browses, and seasons were delineated as follows: May as spring, June–August as summer, September–October as autumn, and November–April as winter if seasons were not clearly indicated and sampling periods were given by months in the comparable studies. Average values across months or years were used in the comparative analysis when diet composition and quality data were given by months and years in some studies. For the comparison of diet quality, a scatter plot showing cluster membership at selected levels of 4 instead of the tree diagram was produced by the SAS ANALYZE macro procedure (SAS 6.0 1989). One-sample *T*-test (Steel and Torrie 1980) was used to determine difference in red deer diet quality between our study area and North American.

Results

Diet composition

Red deer showed significant variation in diet composition among seasons (χ^2 -test: $\chi^2 = 35.9$ for spring-summer, $\chi^2 = 8.2$ for spring-autumn, $\chi^2 = 9.0$ for spring-winter, $\chi^2 = 22.7$ for summer-autumn, $\chi^2 = 22.4$ for summer-winter, $\chi^2 = 10.8$ for autumn-winter; $p < 0.05$ for all comparisons) (Table 1). The diet was dominated by graminoids (46%) in spring, shifted to forbs (45%) in summer, and returned to graminoids (35%) in autumn. Twigs of browses were dominant in the

Table 1. Seasonal composition (%) of red deer diets in the Less Xingan Mountains, northeastern China (1991–1992). Different letters in the same row indicate a significant difference at $p < 0.05$.

Taxa	Spring	Summer	Autumn	Winter
Graminoids				
<i>Carex</i> spp.	36.0	18.1	26.4	< 1.0
<i>Gramineae</i>	10.4	7.0	8.3	< 1.0
Subtotal	46.4 ^a	25.1 ^b	34.7 ^b	1.3 ^c
Forbs				
<i>Oxalis corniculata</i>	6.4	5.5	2.4	–
<i>Caltha palustris</i>	6.4	12.1	4.3	–
<i>Agrimonia pilosa</i>	1.6	21.6	6.7	–
Other	4.4	6.0	12.6	< 1.0
Subtotal	18.8 ^a	45.2 ^b	26.0 ^a	< 1.0 ^c
Browses				
<i>Populus</i> spp.	7.6	12.1	7.7	31.6
<i>Salix</i> spp.	< 1.0	1.5	2.4	9.9
<i>Betula</i> spp.	1.2	2.0	4.3	6.9
<i>Pinus koraiensis</i>	< 1.0	1.5	1.2	13.8
Other	9.2	6.0	11.3	12.1
Subtotal	19.6 ^a	23.1 ^a	26.9 ^a	74.3 ^b
Unknown forbs and browses	4.8	4.0	4.0	1.7
Ferns				
<i>Equisetum hiemale</i>	< 1.0	2.0	20.9	–
Other	6.4	2.0	4.7	1.5
Subtotal	6.8 ^a	2.0 ^a	6.7 ^a	22.4 ^b
Mosses	1.2 ^a	< 1.0 ^a	2.0 ^a	–

winter diet (74%). Red deer consumed more graminoids in spring than in other seasons ($p < 0.05$), and more forbs in summer than in spring and autumn ($p < 0.05$). They maintained a relatively constant level of browses in diets during snow-free seasons ($p > 0.05$). Although ferns were often eaten in small amounts during snow-free seasons, they increased in winter (22%) due to the dramatic increase of horsetail *Equisetum hiemale* in diets ($p < 0.05$). Red deer rarely ate mosses in all seasons.

The majority of forbs eaten during snow-free seasons was *Oxalis corniculata*, *Caltha palustris* and *Agrimonia pilosa*, which comprised 52–87% of the forb component of the diets. *Populus* spp. was an important browse species in all seasons, especially winter. Other principal items in winter diets included *Equisetum hiemale*, *Pinus koraiensis*, *Salix* spp. and *Betula* spp.. Consumption of *Pinus koraiensis* peaked in winter (Table 1).

Forage and diet quality

Concentrations of CP and IVDMD in all types of forages were generally highest in spring, decreased through summer and autumn, and reached their lowest point in winter, whereas contents of fiber components (NDF and ADF) were lowest in spring and increased as plant tissue matured (Table 2). Similarly, from spring through winter dietary CP and IVDMD declined significantly ($r_S = 1$, $p < 0.05$). CP decreased about three-fold from 19.6 to 6.4%, and IVDMD about two times from 61.1 to 32.9% (Table 3). In contrast, dietary NDF and ADF increased consistently through winter. Although a significant seasonal trend existed in dietary NDF ($r_S = -1$, $p < 0.05$) rather than in ADF ($r_S = -0.4$, $p > 0.05$), the magnitude of change in dietary NDF was smaller than ADF.

Dietary Ca and Na increased continually from spring to autumn and then dropped in winter, but dietary P and K showed different patterns and increased from spring to summer, reaching the highest level, and then decreased continually from summer to winter (Table 3). However, no consistent seasonal trends were found in dietary minerals (r_S were -0.4 for Ca, -0.2 for P, 0.2 for Na, and 0.8 for K, $p > 0.05$).

Comparisons of red deer diet composition and quality

Comparisons of red deer diet composition and quality between our region and North America were summarized in Figs 1 and 2. In Fig. 1, 15 studies including this study were plotted together based on the principal component analysis of seasonal diet composition, with the first principal component as X axis and the second principal component as Y axis. The first 2 principal components account for 97% of the variance. The first principal component represents changes in the proportions of graminoids in the diets, decreasing from the left to the right of X axis and the second principal component reflects changes in the proportions of forbs in the diets, rising as values of Y axis increase. Seasonal variation in diet composition was evident from Fig. 1 and a certain similarity existed between our results and those from North America wapiti. A wider variation in diet composition was found in spring than other seasons, whereas a larger similarity existed in summer and autumn diet composition between our study area and North America. Two groups could be identified in the winter diet composition, one located on the low left corner indicating that graminoids were dominant in the diets, the other on the low right corner indicating that browses were staple components in the diets. This study fell in the later and was farthest on the left with over 70% of the diets being browse twigs.

In contrast with wide regional variation in diet composition, red deer in our study area had similar seasonal nutritional quality of diets both in CP contents and IVDMD to those of North American wapiti ($p > 0.05$). The same seasonal changes in red deer diet quality existed between our region and North America (Fig. 2). Exceptionally high and low dietary IVDMD values were reported by

Table 2. Chemical composition of principal forages consumed by red deer in the Less Xingan Mountains, northeastern China (1991–1992). CP – crude protein (%), NDF – neutral detergent fiber (%), ADF – acid detergent fiber (%), IVDMD – *in vitro* dry matter digestibility (%), Ca – calcium (%), P – phosphorus (%), Na – sodium ($\mu\text{g/g}$), K – potassium (%). ^a twigs with leaves in spring, summer, and autumn, and only twigs in winter.

Taxa	Components							
	CP	NDF	ADF	IVDMD	Ca	P	Na	K
<i>Carex</i> spp.								
Spring	15.30	65.80	29.04	62.50	0.26	0.16	187.66	2.23
Summer	10.12	76.75	44.46	59.96	0.22	0.41	144.85	2.11
Autumn	11.56	77.38	47.56	48.72	0.37	0.29	126.59	1.60
Forbs								
Spring	22.18	40.24	20.55	64.30	0.77	0.36	93.66	3.72
Summer	15.04	57.19	42.02	56.59	1.41	0.39	177.32	3.91
Autumn	12.32	56.65	37.76	51.07	2.84	0.42	304.40	2.82
Ferns								
Spring	28.80	64.38	44.99	52.49	0.25	0.40	200.99	3.39
Summer	14.98	71.32	53.50	48.76	0.68	0.28	172.17	2.86
Autumn	9.16	70.08	67.46	39.53	0.87	0.29	121.37	2.71
Browse ^a								
<i>Populus</i> spp.								
Spring	17.87	48.79	33.69	51.84	0.55	0.27	92.84	1.21
Summer	10.20	72.53	61.01	50.17	1.05	0.35	136.24	1.26
Autumn	8.44	78.65	64.27	45.64	1.44	0.43	192.33	1.04
Winter	6.60	72.03	53.67	33.20	0.79	0.32	97.82	1.61
<i>Betula</i> spp.								
Spring	27.90	57.61	39.84	44.06	0.31	0.19	126.06	0.74
Summer	11.19	72.02	49.98	42.15	0.56	0.41	146.85	1.25
Autumn	9.31	60.58	46.93	37.89	0.50	0.23	77.56	0.68
Winter	7.98	66.16	53.62	28.62	0.30	0.37	143.39	0.28
<i>Salix</i> spp.								
Spring	22.69	58.85	44.78	57.63	0.68	0.37	158.90	1.07
Summer	14.65	66.94	53.56	48.32	0.98	0.33	132.61	1.50
Autumn	8.37	65.21	49.69	43.81	1.81	0.17	114.63	1.01
Winter	5.81	72.03	61.46	31.86	0.43	0.37	137.44	0.38
<i>Aralia mandshurica</i>								
Spring	29.79	55.09	20.84	58.83	–	–	–	–
Autumn	5.71	68.41	49.74	39.76	–	–	–	–
Winter	11.48	58.94	46.47	42.29	0.84	0.22	131.44	0.95
<i>Acanthopanax senticosus</i>								
Autumn	6.89	74.37	50.72	42.43	–	–	–	–
Winter	8.67	69.33	52.41	32.58	0.97	0.44	107.54	0.87
<i>Tilia amurensis</i>								
Autumn	5.52	73.25	54.96	45.95	–	–	–	–
Winter	5.14	74.72	58.70	29.78	1.13	0.50	164.43	0.53
<i>Pinus koraiensis</i>								
Winter	5.33	66.01	50.37	34.47	0.18	0.21	65.10	0.42

Table 3. Nutritional quality of red deer diets (on dry matter basis) in the Less Xingan Mountains, northeastern China (1991–1992). See Table 2 for explanations of symbols.

Component	Season			
	Spring	Summer	Autumn	Winter
CP (%)	19.61	13.51	11.55	6.35
NDF (%)	55.64	63.82	67.30	69.91
ADF (%)	27.90	45.50	45.51	54.33
IVDMD (%)	61.14	55.84	48.36	32.91
Ca (%)	0.43	1.04	1.50	0.54
P (%)	0.25	0.39	0.35	0.31
Na (µg/g)	152.00	162.20	197.94	101.56
K (%)	2.60	2.98	1.94	0.99
Ca : P	1.7 : 1	2.7 : 1	4.3 : 1	1.7 : 1
K : Na	171.1 : 1	183.7 : 1	98.2 : 1	97.9 : 1

Hanely (1984) and Leslie *et al.* (1984), respectively. Another extremely high IVDMD value occurred in red deer winter diets of west central Alberta, Canada (Morgantini and Hudson 1985). Interestingly, Leslie *et al.* (1984) reported higher dietary CP values in all seasons except spring than other researchers, whereas

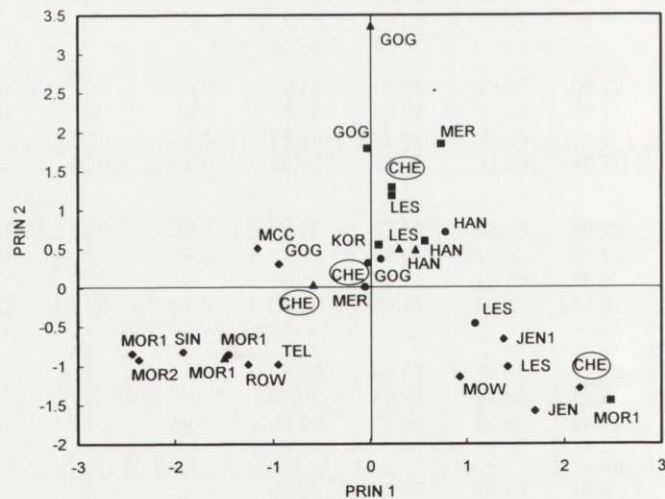


Fig. 1. Principal component analysis of red deer seasonal diet composition in this study region (CHE) and North America (KOR – Korfhage and Nelson 1980, ROW – Rowland *et al.* 1983, HAN – Hanely 1984, LES – Leslie *et al.* 1984, MOR2 – Morgantini and Hudson 1985, JEN1 – Jenkins and Wright 1988, MOR1 – Morgantini and Hudson 1989, MOW – Mower and Smith 1989, JEN – Jenkins and Starkey 1993, MCC – McCorquodale 1993, SIN – Singer and Norland 1994, TEL – Telfer 1994, GOG – Gogan and Barrett 1995, MER – Merrill *et al.* 1995). Triangles – spring, squares – summer, circles – autumn, and diamonds – winter.

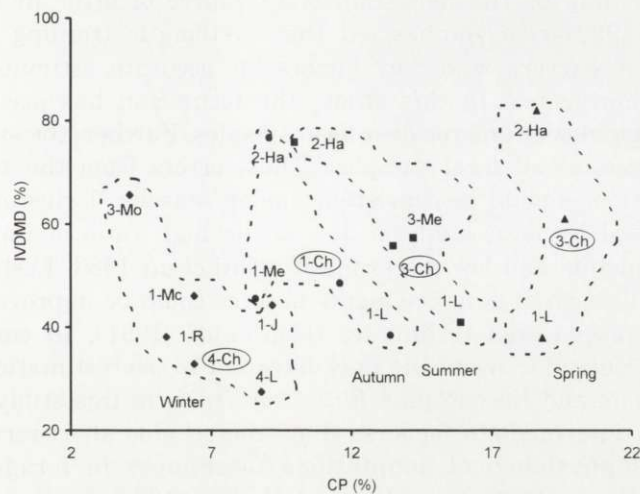


Fig. 2. Crude protein (CP) contents and *in vitro* dry matter digestibilities (IVDMD) of red deer diets in this study region (Ch) and North America (R – Rowland *et al.* 1983, Ha – Hanely 1984, L – Leslie *et al.* 1984, Mo – Morgantini and Hudson 1985, J – Jenkins and Starkey 1993, Mc – McCorquodale 1993, Me – Merrill *et al.* 1995). For Hanely (data from Tables 2 and 3), Morgantini and Hudson (data from Tables 1 and 2), and McCorquodale (data from Tables 1 and 2), CP and IVDMD values were calculated from data in their papers using the same method as in this study. Arabic numbers represent the numbers of clusters in the cluster analysis. Values with the same number of cluster were grouped in the same cluster.

Hanely (1984), and Morgantini and Hudson (1985) reported lower CP values in summer and winter diets. In our study area, red deer has lower dietary IVDMD values in winter than generally reported (Fig. 2).

Discussion

The accuracy of fecal analysis to determine herbivore diet composition has been widely investigated by a number of researchers. Serious problems with this method include (1) technician error (Holechek *et al.* 1982a, b), (2) differential digestibility of plant species (Vavra *et al.* 1978, Leslie *et al.* 1983), (3) low discernibility of epidermal fragments due to lack of identifiable characteristics (Todd and Hansen 1973), and (4) sample preparations (Vavra and Holechek 1980, Holechek *et al.* 1982a). Forbs are often underestimated in fecal analysis because of their high digestibility (Holechek *et al.* 1982b, McInnis *et al.* 1983), but this may not be the case in other studies (Todd and Hansen 1973, Alipayo *et al.* 1992). We assumed that this bias resulted in underestimation of forbs in spring diets in this study because some early spring forbs that were observed to be eaten by red deer in the field were not detected in fecal samples. Holechek *et al.* (1982a) thought that

technician error may be the most important source of error in fecal analysis. Alipayo *et al.* (1992) also emphasized that systematic training and adequate practice by the observers were key factors for accurate estimates of the diet composition of herbivores. In this study, the technician has accumulated over 500 hr analyzing red deer and roe deer fecal samples. Further, the same technician completed analysis of all fecal samples. Thus, errors from the technician and sample preparations should be consistent among seasons. Twigs of browses may be underestimated by fecal analysis due to the high ratio of unidentifiable to identifiable fragments and low discernibility (Gill *et al.* 1983, Leslie *et al.* 1983). However, identification of twig fragments in feces could be improved by selecting proper sample preparation techniques (Gao *et al.* 1991). In contrast, higher discernibility of cuticular fragment may have led to overestimation of the fern, *Equisetum hiemale* and Korean pine *Pinus koraiensis* in this study.

Red deer, as intermediate feeders, show remarkable short-term or seasonal anatomical and physiological adaptations to changes in forage quality and availability (Hofmann 1989, Renecker and Hudson 1990, Spalinger *et al.* 1993, Freudenberger *et al.* 1994). As a result, a high degree of plasticity exists in diet selection of red deer. Results of the present study are consistent with this argument. In our study area, red deer fed mainly on graminoids in spring, shifted to forbs diets in summer when forbs peaked in biomass, and transferred again to graminoids in autumn when availability of forbs dropped to an extremely low level (H. Chen *et al.*, unpubl.) (Fig. 3). The switch from forbs to grasses also was reported by Merrill (1994). Availability of forbs appeared to be a key factor causing these changes in diets as illustrated in Fig. 3. The other important factor may be the quality of forbs. Recently, Fraser (1996) demonstrated that the greater surface enlargement exists within the rumen of red deer, which indicates a lower

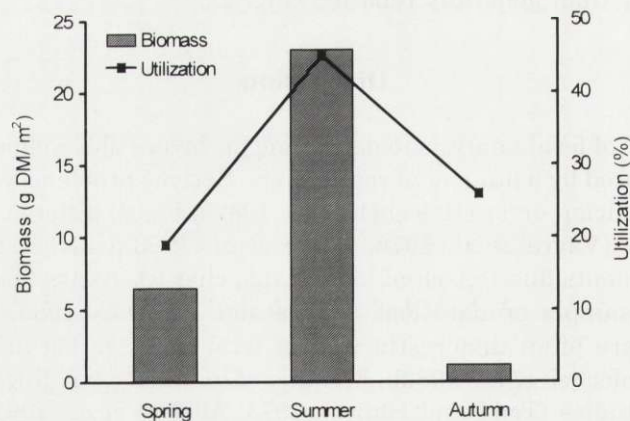


Fig. 3. The biomass and utilization of forbs for red deer in different seasons in the Less Xingan Mountain, Northeastern China (1991-1992).

adaptation to digestion of fibrous forages. Thus, red deer may avoid fiber as long and as much as possible (Hofmann 1989). Although IVDMD was lower in forbs than in grasses during summer, forbs had higher CP, and lower NDF and ADF than grasses (Table 2). Heavy consumption of forbs in summer is likely due to low fiber contents which may lead to rapid cell-wall breakdown and passage rate (Spalinger *et al.* 1986) rather than dry matter digestibility. Merrill (1994) reported that no significant difference was found in IVDMD between forbs and grasses during summer. This result tends to support this hypothesis. We and other researchers (Merrill 1994) observed that red deer mainly selected leaves by stripping them off twigs of shrubs and trees in summer and early autumn. In our study area, leaves of most shrubs and trees fall at the end of September, causing a rapid decline in availability of leaves. Thus, the proportion of browses in autumn diets did not increase significantly compared to summer diets. By switching diets from forbs to grasses in autumn, red deer may intake more energy from grasses because a high ratio of reticulum-rumen to body mass allow red deer to digest the cellulose in grasses more completely (Hanely 1982, Hofmann 1989, Merrill 1994).

Habitat, season, climate, altitude, and latitude are main sources of wide regional variation in deer diet composition (Rowland *et al.* 1983, Tixier and Duncan 1996). In winter, wapiti inhabiting forests mainly fed on browses (Leslie *et al.* 1984, Jenkins and Starkey 1993, Mower and Smith 1989), whereas in grasslands, prairie, and steppe, graminoids were dominant in the diets because chinooks or mild climate keep those study areas largely snow free (Morgantini and Hudson 1985, 1989, Telfer 1994, Gogan and Barrett 1995) (Fig. 1). In spring, wapiti extremely consumed either graminoids (Morgantini and Hudson 1989) or forbs (Gogan and Barrett 1995) in grasslands and coastal prairie, whereas in forests, graminoids, forbs, and browses were relatively equally used by red deer except a little more graminoids in diets in this study (Fig. 1). Whether in grasslands (Gogan and Barrett 1995, Merrill *et al.* 1995) or forests (Leslie *et al.* 1984 and this study), forbs were principal food items in diets during summer. In autumn, habitat cannot explain a large variation in red deer diet composition completely (Fig. 1). Differences in diet composition may have affected diet quality of red deer populations in different habitats. In winter, red deer occupying grasslands had higher dietary IVDMD but lower dietary CP than red deer in forests (Fig. 2). Diets of red deer in grasslands were dominated by grasses which contained much higher IVDMD but lower CP than browses that were principal food items in diets of wapiti in forests (Hobbs *et al.* 1981, Rowland *et al.* 1983, McCorquodale 1993). Thus, it may be assumed that red deer will be more limited by energy in forests than in grasslands during severe winter.

Li and Yan (1989) reported seasonal composition of red deer diets in the Less Xingan Mountains, northeastern China. Their results showed that herbaceous plants dominated spring diets (87%), but more than 85% of diets were composed of browses in other seasons. These results were very different from ours. We suspected that forbs were extremely underestimated or even neglected in their

study because their results were from analysis of only four rumen samples, one in each season. In most studies, including our previous work (Chen and Xiao 1989, Chen *et al.* 1993), contribution of ferns to diets was small and ignored. However, Leslie *et al.* (1984) reported high percentages of fern in spring and winter diets of elk (25–37%). Much use of the horsetail, *Equisetum hiemale*, in this study, probably has two reasons. One is that ferns are easily overestimated because their cuticular fragments usually have higher discernibility (Todd and Hansen 1973). This is particularly true for *E. hiemale* because of its large and easily discernible fragments. The other, maybe more important, is the shortage of forages in winter. In our study area, biomass of forages dropped to the lowest level in winter (22.9 g DM/m² in clearcuts) compared with other seasons (42.3–168.5 g DM/m²) (H. Chen *et al.*, unpubl.). Further, the area of clearcuts as suitable winter feeding habitats (Zhang and Xiao 1990) was smaller because forests have been logged selectively in this region. This was further confirmed by our observation during winter investigation. In January and February, red deer often cratered in snow to feed on green herbaceous plants and ferns. Moreover, bark of *Ulmus* spp. was commonly stripped in February. We measured 31 stripped *Ulmus* trees and found that average diameter at breast height was 4.4 cm (3–8.5 cm), and the mean of the highest stripped points to the ground was 1.8 m (0.5–3 m). Stripping of trees was also reported in eastern Europe (Jamrozy 1980, Matrai and Kabai 1989). Jamrozy (1980) found that red deer stripped bark from 27 tree species and estimated that bark amounted to about 25% of winter diets.

Ammann *et al.* (1973) suggested that 50% digestible dry matter in white-tailed deer diets was required to maintain positive energy balance. In most seasons, dietary IVDMD of red deer in this study area was greater than or close to this threshold except in winter (Table 3). Thus, we can infer that red deer would maintain a positive energy balance in snow-free seasons, but in winter energy probably become an important limiting factor. There is limited information on the protein nutrition at various physiological stages. Until recently, protein requirements for growth and production of red deer have to be extrapolated from domestic ruminants using the factorial approach. For red deer hinds, dietary CP contents for growth and production increase from 10% in autumn/winter (dry) to 17% in summer (lactation), and for stags, from 10% in autumn/winter to 12% in spring/summer (Adam 1991). Therefore, dietary CP contents of 12–20% during snow-free seasons in our study area are generally considered adequate for meeting protein requirements during period of growth and production. CP content in winter diets (6%) exceeded generally accepted 5–5.7% for meeting metabolic nitrogen requirements (Maloiy *et al.* 1970, Mould and Robbins 1981, Nelson and Legee 1982) but was lower than 10% needed for growth (Adam 1991). Digestion of protein can be influenced by soluble phenolics, like tannins, which bind protein to form irreversible complexes, thereby reducing protein availability and digestibility of cell solubles (Robbins *et al.* 1987a, b). Thus, concentrations of secondary plant compounds in forages may alter the relative value of diet quality. However,

salivary protein of red deer may have a high capacity to bind tannins, hence reducing effects of tannins (Hagerman and Robbins 1993).

Deficiencies and imbalances of minerals affect animal condition, fertility, productivity, and mortality (Robbins 1983). Recently, the importance of mineral nutrition has received considerable attention in diet selection, spatial distribution and seasonal movement of wild herbivores at population and ecosystem level (Bazely 1989, McNaughton 1988, 1990). However, information on mineral nutrition in cervids has been very limited. In our study, dietary K was higher in spring and summer than in autumn and winter (Table 3). This pattern was reported by Weeks and Kirkpatrick (1976) for white-tailed deer. Similarly, Leslie *et al.* (1984) observed the same pattern for P content in elk diets. In contrast, dietary Ca, P and Na in this study were higher in summer and autumn, and lower in spring and winter (Table 3). Dietary Ca to P ratios ranging from 1:1 to 2:1 are considered to be ideal for proper absorption and metabolism (Robbins 1983). Dietary ratios of Ca to P fall in these optimal ranges in spring and winter (1.7:1), but deviate from the ideal ratios in summer (2.7:1), and especially in autumn (4.3:1) in this study. However, excesses of Ca may have a far lesser effect on P absorption than do excesses of P on Ca absorption (Robbins 1983). Weeks and Kirkpatrick (1976) suggested that high intake of K led to excessive Na loss and a temporary negative Na balance. However, Christian (1989) found that Na loss and balance were not significantly affected by high dietary K content in small mammals. In this study, K : Na ratios (Table 3) are much lower than reported by Weeks and Kirkpatrick (1976) for white-tailed deer (156–485). Thus, the problem of high dietary K content resulting in Na loss and imbalance might not be serious, even if it occurred in red deer.

We know little about requirements for Ca, P, Na and K in wild large herbivores. Some information has to be obtained from domestic ruminants. Until recently, the only available data for Ca requirements are 0.37% for red deer (Muir *et al.* 1987, the average of two individuals, calculated from rates of Ca deposition in the antlers and net fecal endogenous losses) and 0.4–0.64% for white-tailed deer reported by McEwen *et al.* (1957) and Ullrey *et al.* (1973). Recently, Grasman and Hellgren (1993) reported the lower P requirements (0.11–0.16%) for white-tailed deer than the generally accepted value of 0.20–0.25% for mule deer reported by Short (1981). Pletscher (1987) indicated that minimum Na requirements were 0.017–0.038% for white-tailed deer, far lower than the estimate for domestic ruminants, 0.1–0.2% (Maynard *et al.* 1979). Robbins (1983) also suggested that Na requirements of birds and mammals would reach 0.05–0.15% during growth and reproduction. Maynard *et al.* (1979) reported that critical level of K was 0.20–0.30% for domestic ruminants. Therefore, according to above data, we can infer that Ca, P, K in seasonal red deer diets are adequate in most cases, but Na might appear deficient throughout the year.

It is concluded that diet of red deer in our region is characteristic of mixed feeders (Hofmann 1989). The diet of our red deer undergoes to similar seasonal

changes in quality as that of North American wapiti. Although red deer have enough protein in most seasons, energy may be a key limiting factor in severe winters.

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