

## Dietary niche relationships among cervids relative to winter snowpack in northwestern Montana

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We compared diets of white-tailed deer (*Odocoileus virginianus ochrourus*), Rocky Mountain elk (*Cervus elaphus nelsoni*), and Shiras moose (*Alces alces shirasi*) during two winters in the North Fork of the Flathead Valley, Montana. Diets of white-tailed deer contained the greatest proportions of low-lying evergreen shrubs, as well as high proportions of coniferous browse. Elk selected greater proportions of grasses than did white-tailed deer or moose, whereas moose consumed the greatest proportion of deciduous shrubs. Deep snow in 1982 increased the similarity of diets chosen by white-tailed deer, elk, and moose. In 1982, white-tailed deer and elk consumed more total browse, and moose more coniferous browse, as deep snow covered the preferred forages. Increased dietary overlap and energy limitations suggested a potential for interspecific competition during harsh winters.

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Nous avons comparé les régimes alimentaires chez des Cerfs de Virginie (*Odocoileus virginianus ochrourus*), des Wapitis (*Cervus elaphus nelsoni*) et des Orignaux (*Alces alces shirasi*) durant deux hivers dans la vallée de la branche nord de la Flathead au Montana. Ce sont les régimes alimentaires des Cerfs de Virginie qui contenaient les proportions les plus élevées d'arbrisseaux bas à feuilles permanentes et ils contenaient aussi de grandes quantités de conifères. Les Wapitis consommaient de plus grandes proportions d'herbages que le Cerf de Virginie ou l'Orignal, alors que c'est l'Orignal qui a consommé la plus grande quantité d'arbrisseaux à feuilles décidues. En 1982, la couche de neige particulièrement épaisse a augmenté la similarité entre les régimes des trois Cervidés. Durant cette année, les Cerfs de Virginie et les Wapitis ont consommé plus de nourriture en tout et les Orignaux ont mangé plus de conifères, car la neige avait recouvert les plantes préférées. Le chevauchement plus grand des niches alimentaires et les limites énergétiques accrues permettent de croire à l'existence d'une compétition interspécifique durant les hivers plus rigoureux.

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### Introduction

Although there have been several investigations comparing diet selection within ungulate communities (Hanley and Hanley 1982; Hobbs *et al.* 1983; Schwartz and Ellis 1981), the influence of forage availability on dietary niches of cervids is poorly understood. Optimal foraging theory suggests that individuals should forage selectively when food is abundant, and opportunistically when forage is of more uniform, lower quality and less abundant (Nudds 1980; Pyke *et al.* 1977; Westoby 1974). Others have reasoned that species should realize their optimum feeding niches when forage is limiting, and competition or other selective forces promote maximally efficient foraging (Schoener 1982; Wiens 1977; Hobbs *et al.* 1983). Opportunistic foraging patterns would lead to high dietary overlap, whereas specialized diets, narrowed by competition, would promote dietary divergence during nutritionally lean periods (Wiens and Rotenberry 1979: p. 285).

Recent studies of ungulate diets in sympatry provide evidence for both dietary specialization and opportunism during periods of resource scarcity. The majority of studies have reported that dietary divergence coincided with nutritionally lean seasons, suggesting that greater food specialization occurred during periods of resource shortage (Dailey *et al.* 1984; Hansen and Reid 1975; Hobbs *et al.* 1983; Olsen and Hansen 1977; Spowart and Hobbs 1985; Willms *et al.* 1980). Others have reported that greater dietary overlap occurred during lean than during rich periods, suggesting opportunistic feeding and a potential for interspecific competition (Anthony and Smith 1977; Leslie *et al.* 1984; Singer 1979; Schwartz and Ellis 1981).

In this paper we describe midwinter diets of white-tailed deer, Rocky Mountain elk, and Shiras moose during consecutive severe and mild winters in Glacier National Park, Montana. Our objective was to determine if deep snow in the Rocky Mountains influenced overlap and nutritional quality of cervid diets.

### Study area and methods

Winter diets were investigated during 1982 and 1983 along the North Fork of the Flathead River on the western boundary of Glacier National Park (48°47' N, 114°16' W). The study area provides low elevation winter range for white-tailed deer, elk, and moose that summer within Glacier National Park to the east and Flathead National Forest to the west. Although cervids are harvested annually on the National Forest, large population segments are protected within the National Park and appear to be at habitat carrying capacity. Snowpack during 1982 (100 cm) was 143% of the long-term mean ( $\bar{X}$  = 70 cm, United States Weather Service, Polebridge, Montana), whereas snow depths in 1983 (50 cm) were only 71% of average.

The study site consists of a mosaic of active floodplains, older alluvial terraces, and glaciated uplands. Elevations range from 1024 m on the river floodplain to 1300 m on an adjoining glacial moraine. Vegetation on the floodplain encompasses pioneer communities at river's edge, midseral black cottonwood (*Populus trichocarpa*) communities on older terraces, and climax spruce (*Picea engelmannii* × *glauca* hybrid) forests on the oldest, infrequently flooded surfaces (Lee 1983). Lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), or subalpine fir (*Abies lasiocarpa*) forests occur on older alluvial terraces and uplands. Grasslands and wetlands are interspersed among the forest communities.

Botanical composition of cervid diets was determined through microhistological analyses of fecal samples. Each sample was a composite of 5 g of fresh fecal material collected from each of 15–20 pellet groups during February 1982 and 1983. Composite samples were

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TABLE 1. Mean percentages ( $N = 3$ ) of principal forage species in winter diets of white-tailed deer, elk, and moose in the North Fork of the Flathead River drainage, 1982–1983, as determined from relative cover of identifiable fecal fragments<sup>a</sup>

	White-tailed deer				Elk				Moose			
	1982		1983		1982		1983		1982		1983	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
<b>Graminoids</b>												
<i>Agropyron spicatum</i>	T <sup>b</sup>		T		T		1	0.7	0		0	
<i>Bromus</i> spp. <sup>c</sup>	0		0		2	0.7	0		0		0	
<i>Calamagrostis rubescens</i>	T		T		1	0.8	2	0.9	0		0	
<i>Carex</i> spp. <sup>c</sup>	1		3	2.2	11	6.2	14	5.0	0		T	
<i>Elymus glaucus</i>	0		0		0		3	2.7	0		0	
<i>Festuca idahoensis</i>	0		0		1	0.3	1	0.5	0		0	
<i>Festuca scabrella</i>	T		1	0.3	1	0.8	3	1.6	0		0	
<i>Poa</i> spp. <sup>c</sup>	1	0.6	1	0.3	2	0.6	2	0.9	0		0	
Subtotal	2	0.6	5	2.0	17	5.9	26	4.5	0	T		
<b>Deciduous shrubs</b>												
<i>Amelanchier alnifolia</i>	T		0		0		0		1	1.2	2	0.9
<i>Alnus incana</i>	T		0		0		0		0		T	
<i>Cornus stolonifera</i>	13	6.4	8	2.6	22	9.4	16	4.8	25	1.9	47	10.5
<i>Elaeagnus/Shepherdia</i> <sup>d</sup>	4	2.5	2	1.4	3	2.1	2	1.6	1	0.7	T	
<i>Populus trichocarpa</i>	13	8.7	5	2.5	2	1.0	3	0.2	T		0	
<i>Ribes</i> spp. <sup>c</sup>	0		2	1.6	0		0		0		0	
<i>Rubus</i> spp. <sup>c</sup>	8	2.6	5	3.1	15	6.1	8	1.7	8	1.2	8	1.8
<i>Salix</i> spp. <sup>c</sup>	1	0.5	T		5	0.8	6	1.6	18	4.7	22	6.2
Subtotal	40	17.2	22	7.1	46	10.7	36	5.6	53	5.8	79	17.1
<b>Evergreen subshrubs</b>												
<i>Cornus canadensis</i>	0		1	0.4	0		0		0		0	
<i>Berberis repens</i>	4	1.9	19	4.0	1	0.3	6	3.0	0		T	
<i>Vaccinium</i> spp. <sup>c</sup>	1	0.2	0		0		0		0		0	
Subtotal	6	2.0	19	4.2	1	0.3	6	3.0	0		T	
<b>Conifers</b>												
<i>Abies lasiocarpa</i>	5	2.9	10	5.9	5	0.9	4	2.5	28	3.0	11	7.6
<i>Juniperus</i> spp. <sup>c</sup>	9	5.3	11	6.0	3	3.0	9	1.4	T		0	
<i>Picea</i> spp. <sup>c</sup>	5	2.8	0		4	1.4	0		T		0	
<i>Pinus contorta</i>	11	4.8	10	5.4	8	2.7	8	2.8	4	1.2	3	2.9
<i>Pseudotsuga menziesii</i>	18	9.1	20	4.2	16	5.3	9	6.6	15	3.2	7	6.5
Subtotal	49	19.1	51	6.7	36	6.3	30	8.0	47	5.8	21	16.9
<b>Other taxa</b>												
<i>Athyrium filix-femina</i>	0		2	1.7	0		T		0		0	
<i>Equisetum arvense</i>	2	0.9	1	0.8	T		2	1.2	0		0	
Lichens	1	1.1	0		T		0		T		0	
Subtotal	3	0.8	3	2.4	T		2	1.4	T		0	

<sup>a</sup>Principal forages made up of at least 2% of any cervid diet.<sup>b</sup>T, trace (<0.5%).<sup>c</sup>Species were not distinguished.<sup>d</sup>*Elaeagnus commutata* and *Shepherdia canadensis* were indistinguishable in the feces.<sup>e</sup>Spruce hybrid (*P. engelmannii* × *glauca*).

collected from three independent study blocks for each species each year, resulting in 18 dietary determinations (i.e., 3 cervid species × 2 years × 3 replicates). Fecal samples were stored frozen until they were analyzed (Wildlife Habitat Management Laboratory, Washington State University, Pullman), at which time they were broken apart by agitating with water at low speed in a household blender (1–2 min). Samples were washed over a 200-mesh screen, soaked in bleach (5–10 min) to remove pigments, and dyed in lactophenol blue before being mounted on microscope slides for analysis. Botanical composition of diets was expressed as percent relative cover of identifiable plant epidermal and cuticle fragments in 300 random microscope fields. Forage fragments were identified at 400× magnification by comparing them with reference plant microscope slides. Measurements of relative cover were made at 100× magnification using a gridded eyepiece.

Fifteen forage species were collected concurrently with fecal

samples in each of the three study blocks during 1983. Only plant part consumed by cervids were collected, as determined by inspecting adjacent browsed plants. Samples of each forage species were composited across sampling blocks, oven-dried at 50°C, ground through a 1-mm sieve, and stored in air-tight plastic bags prior to nutritional analyses. Crude protein (CP, Kjeldahl total N × 6.25) and in vitro digestible dry matter (IVDDM, Tilley and Terry 1963) were determined in duplicate and expressed as means on a 100% dry matter basis. Inoculum for IVDDM estimates was obtained from a captive fistulated elk fed a commercial pelleted ration (18% CP, 60% IVDDM) and low-quality pasture hay. Effects of a single inoculum source may have influenced interspecific dietary comparisons. However, logistic and sampling problems prevented obtaining inoculum from separate donor species. Because rank orders of forage digestibilities are often influenced by donor sources (Campa *et al.* 1984; Hjeljord *et al.*

TABLE 2. Overlap indices (OI) and Spearman rank correlations (Rho) of mean seasonal diets of white-tailed deer (WTD), elk, and moose in the North Fork of the Flathead River drainage, winters 1982–1983 (rank correlations are test statistics for significant dietary associations between species<sup>a</sup>)

	Species pairs			Average
	WTD–elk	WTD–moose	Elk–moose	
1982				
OI	0.81	0.57	0.71	0.70
Rho	0.73 <sup>b</sup>	0.52 <sup>b</sup>	0.67 <sup>b</sup>	
1983				
OI	0.71	0.33	0.57	0.54
Rho	0.68 <sup>b</sup>	0.25	0.56 <sup>b</sup>	
Average OI	0.76	0.45	0.64	0.62

<sup>a</sup>Rank correlations are based on principal forages (>2% in diet) common to the diets of both species.

<sup>b</sup>Significant dietary association between species ( $P < 0.05$ ).

1982), it appeared justified to use a single source of inoculum for annual dietary comparisons.

Nutrient compositions of cervid diets were calculated from nutrient contents of principal forage species weighted by their proportional contributions to each diet (Leslie *et al.* 1984). Principal forages were defined as plant species that made up at least 2% of any cervid diet. Occasionally, principal forages that occurred in a diet were not collected or analyzed nutritionally. In those cases, average values for a forage class (e.g., grasses, deciduous shrubs, conifers, subshrubs) were substituted for specific values. Other taxa, including ferns, horsetails (*Equisetum spp.*), and lichens, were omitted from dietary analyses because they were not evaluated nutritionally, and together they made up less than 3% of any cervid diet.

Similarities of cervid diets were assessed using Morisita's index of dietary overlap as modified by Horn (1966), and Spearman's rank order correlation coefficient. Botanical and nutritional characteristics of diets were compared among cervid species and between years using two-factor analyses of variance with three replicates in each cell. Additionally, dietary characteristics for individual cervid species were compared between years using *t*-tests. Newman-Keul's procedure was used to detect dietary differences between pairs of cervid species ( $P < 0.05$ ) (Kirk 1982: p. 123).

## Results

### Botanical composition of diets

Deciduous shrubs and conifers dominated winter diets of North Fork cervids (Table 1). Red-osier dogwood (*Cornus stolonifera*) was an important dietary component of each cervid species. Additionally, cottonwood, creeping Oregon grape (*Berberis repens*), junipers (*Juniperus spp.*), lodgepole pine, and Douglas-fir were important dietary items of white-tailed deer. Sedges (*Carex spp.*), *Rubus spp.*, and Douglas-fir were important winter elk forages, whereas willows (*Salix spp.*) and subalpine fir were the main dietary staples of moose. Averaged over both winters, white-tailed deer consumed more Oregon grape than did elk or moose ( $P < 0.01$ ); however, the magnitude of the difference varied between years (year  $\times$  species interaction,  $P = 0.01$ ). Elk consumed more grasses than did deer or moose, which ate only trace amounts ( $P < 0.01$ ). Moose ate the greatest amount of deciduous shrubs ( $P < 0.03$ ). There was no significant difference in the amount of coniferous browse eaten by cervids ( $P = 0.29$ ), but white-tailed deer tended to eat the most coniferous browse.

White-tailed deer and elk diets differed between years (Table 1). Both species consumed more Oregon grape (deer,  $P = 0.04$ ; elk,  $P = 0.02$ ) and less total browse (deer,  $P = 0.01$ ; elk,  $P =$

0.07) in 1983, a mild winter, than in 1982, a harsh winter. Elk tended to eat more grass during the milder winter, but that difference was not significant ( $P = 0.28$ ). Moose tended to eat more deciduous and less coniferous browse during the milder winter, although that difference also was not significant ( $P = 0.21$ ).

Interspecific dietary relationships varied among cervid species pairs and between years (Table 2). Dietary overlap between white-tailed deer and moose was lower than for species pairs involving elk. Dietary choices of elk were significantly associated with those of white-tailed deer and moose during both winters (Table 2). Dietary overlaps were less during the mild winter of 1983 than during 1982 for all species combinations.

### Dietary quality

Grasses, shrubs, and coniferous forages differed in nutritional components (Table 3). Oregon grape was highest in CP and IVDDM. Cured grasses were low in CP and high in IVDDM as compared with deciduous shrubs and coniferous browse, which were intermediate in CP and low in IVDDM.

Winter diets of cervids differed in CP ( $P = 0.01$ ), but not in IVDDM ( $P = 0.33$ ). Diets of white-tailed deer contained a higher level of CP than diets of elk and moose (Table 4), which reflected a greater consumption of conifers and Oregon grape by deer. Diets of moose tended to have the lowest level of IVDDM, which reflected a high consumption of deciduous woody browse.

Collectively, IVDDM of cervid diets was greater during a mild winter than during a comparatively snowy winter ( $P = 0.04$ ). Dietary CP tended to be higher during the comparatively mild winter, though the difference only approached significance for white-tailed deer ( $P = 0.16$ ).

## Discussion

Microscopic fecal analyses have been used widely for studies of cervid food habits, but results may be biased by the differential fragmentation and digestibility of forages (Holechek *et al.* 1982). Our determinations of diet composition based on coverage of plant fragments in unground fecal samples minimized biases associated with differential fragmentation during sample preparation. However, proportions of highly digestible forbs and low-lying evergreen shrubs in cervid feces may have underrepresented true dietary proportions. Such forages were largely unavailable under snowpack during our

TABLE 3. Crude protein and in vitro digestible dry matter contents (% of dry matter) of important winter forages of white-tailed deer, elk, and moose in the North Fork of the Flathead River Drainage<sup>a</sup>

	Crude protein	In vitro digestible dry matter
Graminoids		
<i>Carex</i> spp.	7.7	54.4
<i>Elymus glaucus</i>	2.5	36.6
<i>Bromus</i> spp.	6.2	44.0
$\bar{X}$ (SE)	5.5 (1.5)	45.0 (5.2)
Deciduous shrubs		
<i>Amelanchier alnifolia</i>	6.2	36.1
<i>Cornus stolonifera</i>	5.8	41.8
<i>Elaeagnus commutata</i>	11.0	20.8
<i>Populus trichocarpa</i>	6.9	53.7
<i>Rubus</i> spp.	6.8	29.0
<i>Salix</i> spp.	6.8	31.8
$\bar{X}$ (SE)	7.2 (0.8)	35.5 (4.5)
Evergreen subshrubs		
<i>Berberis repens</i>	10.3	57.0
Conifers		
<i>Abies lasiocarpa</i>	7.1	35.9
<i>Juniperus</i> spp.	9.3	49.2
<i>Picea</i> spp.	6.0	
<i>Pinus contorta</i>	7.6	17.0
<i>Pseudotsuga menziesii</i>	6.8	30.0
$\bar{X}$ (SE)	7.4 (0.6)	33.0 (6.7)

<sup>a</sup>Important forages made up >2% of any cervid diet.

TABLE 4. Mean dietary levels ( $\pm$ SE,  $N = 3$ ) of crude protein and in vitro digestible dry matter (% of dry matter) for white-tailed deer, elk, and moose in the North Fork of the Flathead River drainage, winters 1982–1983<sup>a</sup>

Cervid species	Crude protein		In vitro digestible dry matter	
	1982	1983	1982	1983
White-tailed deer	7.3 (0.2)	7.9 (0.2)	36.9 (3.1)	39.6 (2.2)
Elk	6.9 (0.3)	7.1 (0.1)	36.5 (0.5)	40.4 (1.6)
Moose	6.7 (0.1)	6.7 (0.4)	34.4 (0.2)	37.7 (0.5)

<sup>a</sup>Means were derived from nutrient contents of principal forage species weighted by their proportional contribution in each of three replicate diets.

study. Additionally, if similar digestibility biases occurred among species and between years, differences in diets of white-tailed deer, elk, and moose would not be obscured.

Annual differences in deer and elk diets coincided with changes in snow depth and forage availabilities. In 1983, deer were observed digging through 20 cm of fresh snow and elk through 58 cm to obtain Oregon grape and grasses, respectively. When those preferred forages were unavailable under deeper snow, as in 1982, deer and elk consumed more deciduous and coniferous browse. Previous studies reported that Oregon grape made up 71% of the diet of white-tailed deer during early winter, prior to snowfall (Martinka 1970), and grasses made up 70% of the diet of elk during an especially mild North Fork winter (snow depth = 20 cm) (Singer 1979). Results of those studies compared with ours demonstrate the potential magnitude of dietary shifts relating to snowpack.

Moose diets did not differ between years, but tended to

contain a greater proportion of coniferous browse and less deciduous browse during a snowy winter. Availability of deciduous browse in North Fork shrub communities decline from 244 kg dry matter/ha in 1983 to 146 kg/ha in 1988 (K. J. Jenkins, unpublished data). Efficiency of moose foraging is reduced 50% below the maximum at such a low forage availability, causing moose to forage less selectively (Renecke and Hudson 1986). Increased consumption of conifers by moose has been reported previously when deep snow reduce the availability of deciduous browse (Peek 1974).

Increased consumption of browse during a snowy winter increased the dietary similarities among white-tailed deer, elk and moose. Dietary overlaps between species were greater during a snowy winter (57–81%) than during a mild winter (33–71%). Dietary overlaps between white-tailed deer and elk in our study (71–81%) were less than between black-tailed deer and Roosevelt elk in coastal old-growth forests (circa 78–93%, Leslie *et al.* 1984), but they were in the high range of values previously reported for other sympatric native ungulates (74–84%, Anthony and Smith 1977; 3–48%, Hansen and Reid 1975; 41%, Ludwig and Bowyer 1985; 30–50%, Leuthold 1978; and 15–60%, Schwartz and Ellis 1981). Low dietary overlaps (17–57%) reported for the North Fork cervids during a mild winter in 1975 corroborated the effect of snowpack on dietary overlap (Singer 1979).

High dietary overlap during 1982 contradicted the hypothesis that specialized foraging patterns would coincide with nutritionally limiting periods (Schoener 1982). In the North Fork variable snowpack and forage availabilities promoted opportunistic rather than specialized winter foraging behaviour. Low evergreen shrubs, grasses, and forbs simply were not available during periods of deep snow to permit high levels of food specialization and partitioning. We surmised that selective foraging during winter may be favored in relatively snow-free environments where several forage classes are available for partitioning (Dailey *et al.* 1984; Hansen and Reid 1975; Hobbs *et al.* 1983; Olsen and Hansen 1977), and where relatively constant selection pressures promote ecological divergence.

The second study objective was to determine if botanical differences influenced nutrient levels of winter diets. Dietary IVDDM was less during a snowy than a mild winter, but there were no annual differences in dietary CP. Those findings are based on the assumption that cervids selected the same plant parts during both winters. Previous studies suggest that cervids may browse twigs of larger diameter and of lower nutrient content when forage is more limiting (Crête 1976). Selection for coarser twigs was not evident during a severe winter in the North Fork based on measurements of total browse utilization (K. J. Jenkins, unpublished data). However, localized differences in browsing pressure were difficult to detect and may have augmented nutritional differences between years.

Dietary IVDDM of cervids in the North Fork (29–40%) was roughly comparable to that of Colorado mule deer (*O. hemionus hemionus*) (24–37%, Bartmann 1982) and elk (35–47%, Hobbs *et al.* 1981), but was higher than that for black-tailed deer (*O. h. columbianus*) and Roosevelt elk (*C. e. roosevelti*) (26–29%, Leslie *et al.* 1984), and was lower than that for moose in Alberta (44%, Renecker and Hudson 1985), or black-tailed deer (*O. h. sitkensis*) in Alaska (38–58%, Hanley and McKendrick 1985). Undoubtedly, some of that variability was related to methodological differences between studies and sources of rumen inoculum (Milchunas and Baker 1982). However, our results agree with the majority of findings from northern winter ranges:

IVDDM was below the estimated 50% necessary to meet maintenance energy requirements of cervids (Ammann *et al.* 1973), especially when deep snow reduced the availability of low-lying forages. CP levels in the North Fork (6.6–7.7%) were marginally adequate for winter maintenance assuming a winter requirement of 5–9% and that plant secondary compounds did not appreciably reduce protein assimilation.

Low dietary quality and high overlap coupled with high browsing pressure (K. J. Jenkins, unpublished data) suggested that there was a potential for competition between elk and white-tailed deer or moose during severe winters. Niche separation along a spatial gradient could ease such competition, but deep snow reduced available winter range and promoted greater use of mature coniferous forests by cervids (Jenkins 1985). Any adverse effects of forage competition would be most pronounced during consecutive severe winters when cervids are energetically stressed. Variable winter weather and transient forage availabilities would generally ameliorate competition intermittently, both within and between years, and may enhance stable coexistence (Wiens 1977). Furthermore, high quality summer and fall forages would reduce nutritional deficiencies, and may be an important factor promoting faunal diversity in nutritionally deficient winter environments.

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