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Dietary overlap among cattle and cervids in northern Idaho forests

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Abstract

Botanical composition of diets and dietary overlap were investigated among free-ranging cattle (*Bos taurus*), Rocky Mountain elk (*Cervus elaphus nelsoni*), and white-tailed deer (*Odocoileus virginianus*) in coniferous forests of northern Idaho. The study was conducted within the *Abies grandis/Clintonia uniflora* (grand fir/queencup beadlily) and *Thuja plicata/Clintonia uniflora* (western redcedar/queencup beadlily) habitat types. Botanical composition of ungulate diets was determined via microhistological analysis of fresh fecal samples collected in early summer, mid-summer, and early fall of 1987 and 1988. Dietary overlap was examined using Kulcyznski's similarity index. This formula also was used to compare the botanical composition of ungulate diets vs. plant community composition at 5 different seral stages: herb-shrub, sapling, pole, mature, and potential natural community. Cattle consumed graminoid-dominated diets from within early successional communities. Elk also foraged predominantly on graminoids, but elk foraging habits were more diverse and more variable amongst seasons than cattle. White-tailed deer diets were dominated by forbs and shrubs from within late successional communities. Competition for forage between cattle and elk was more likely in the grand fir habitat type, while forage competition between elk and white-tailed deer was more likely in the redcedar habitat type. There was little evidence of potential forage competition between cattle and white-tailed deer in either habitat type.

Key Words: interspecific competition, diet selection, resource partitioning, elk, white-tailed deer, *Bos taurus, Cervus elaphus, Odocoileus virginianus, Abies grandis, Thuja plicata*

Potential natural communities of coniferous forests in northern Idaho are typically close-canopied stands with limited understories (Cooper et al. 1991). Timber harvesting, prescribed burning, and wildfire open these canopies and greatly increase forage production for wild and domestic ungulates; adjacent forest stands provide ungulates with thermal and security cover (Leege 1968, 1969; Irwin and Peek 1983). Successfully integrating ungulate use with timber and fire management activities in these ecosystems requires knowledge of ungulate foraging habits in relation to the forests' successional stages. Resource managers need to know which forage species and which successional plant communities are used by ungulates in each season. Knowledge of foraging habits also is needed to successfully integrate use amongst the different ungulate species present.

Cattle (*Bos taurus*), Rocky Mountain elk (*Cervus elaphus nelsoni*), and white-tailed deer (*Odocoileus virginianus nelsoni*) are the 3 most common ungulates found within the forest ecosystems of northern Idaho. Forest ecosystem management is presently hindered by the lack of research documenting the foraging relationships amongst these ungulates. One previous study examined relationships between cattle and white-tailed deer and found that although cattle and white-tailed deer both consumed large amounts of browse, cattle use was not detrimental to the forage supply of white-tailed deer because there was ample browse available (Thilenius and Hungerford 1967). Hanley (1984) compared diets of Rocky Mountain elk and Columbian black-tailed deer (*Odocoileus hemionus columbianus*) in coniferous forests of western Washington. The potential natural community in these forests was western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and Cascade fir (*Abies amabilis* (Dougl.) Forbes). Large proportions of both elk and black-tailed deer diets were comprised of shrubs and trees, especially in winter. Elk did consume more grasses than did black-tailed deer, while black-tailed deer consumed more browse than did elk. Similar patterns of diet selection were found by Leslie et al. (1984, 1987) when they compared diets of black-tailed deer and Roosevelt elk (*C. e. roosevelti*) in the western Cascade Mountains of Washington. The potential natural community in these forests was codominated by western hemlock and Sitka spruce (*Picea sitchensis* (Bong.) Carr.). Jenkins and Wright (1987, 1988) examined dietary overlap between Rocky Mountain elk and white-tailed deer during winter in coniferous forests of northwestern Montana. These studies found that elk and white-tailed deer consumed mostly shrubs and conifers in a severe winter with deep snowpack, but elk consumed more graminoids in a milder winter when less snowpack made more graminoids accessible.

Any 2 species of sympatric ungulates can interact in 1 of 5 different ways: 1) neutralism, in which neither species affects the other; 2) direct interference, in which both species inhibit each other; 3) amensalism, in which 1 species is inhibited and the other not affected; 4) commensalism, in which 1 species is bene-

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fited while the other is not affected; and 5) protocooperation, in which the interaction is favorable to both species (Odum 1971).

The type of interaction that occurs between any 2 species of ungulates depends upon many site-specific conditions. Influential factors include animal ages and life cycle stages, animal densities (including humans and other predators), animal physiological status, animal and plant health, plant community structure and composition, grazing intensity, and grazing season. Therefore, interspecific relationships that are competitive (i.e., amensalism or direct interference) under 1 set of conditions may be benign (i.e., neutralism) or beneficial (i.e., commensalism or protocooperation) under a different set of conditions (Mosley 1994).

Despite the existence of these different forms of interspecific relationships, it is impossible to definitively ascertain which form is occurring between any 2 species of free-ranging ungulates. This is because the only way to determine the relationship is to compare actual niche breadth vs. virtual niche breadth (Colwell and Futuyma 1971), and such a comparison is physically impossible to accomplish under natural conditions. This fact limits ungulate ecologists to merely gathering circumstantial evidence upon which to base educated guesses about interspecific relationships. For example, even if 2 species of ungulates consume diets of identical botanical composition and even if the animals harvest this vegetation from within the same plant communities, all 5 forms of interspecific relationships remain plausible. Our study examined circumstantial evidence addressing foraging relationships amongst cattle, Rocky Mountain elk, and white-tailed deer in coniferous forests of northern Idaho. Nutritional theory suggests that large-bodied ruminants will forage differently from small-bodied ruminants because as the body size of ruminants increases, weight-specific metabolic rate decreases and weight-specific gut capacity remains constant (Demment and Van Soest 1985). Accordingly, we hypothesized that cattle and elk would consume diets of similar botanical composition from similar seral plant communities, and that neither cattle nor elk would overlap significantly with white-tailed deer.

Study Area

The study area's vegetation consisted of a mosaic of seral stages. This mosaic was largely created by timber harvesting. The study area was used as summer range (usually May - October/November, depending on snow conditions) by cattle, elk, and white-tailed deer that wintered at lower elevations. The cattle (i.e., cow/calf pairs) stocking rate was moderate (i.e., 40–60% utilization on primary suitable range) and the distribution, timing, and frequency of forage utilization by cattle was only minimally influenced by the presence of fences and herding. The botanical composition of diets and dietary overlap were studied among cattle, elk, and white-tailed deer within 2 different habitat types. For clarity, these 2 habitat types are presented as Study 1 and Study 2.

Study 1 was conducted within the *Abies grandis/Clintonia uniflora* (grand fir/queencup beadlily) habitat type, one of the major habitat types of northern Idaho (Cooper et al. 1991). The potential natural community is dominated by grand fir (*Abies grandis* (Dougl.) Forbes) and Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco). Common herbs include queencup beadlily (*Clintonia uniflora* (Schult.) Kunth.), starry solomon-plume (*Smilacina stellata* (L.) Desf.), and sweetscented bedstraw (*Galium triflorum* Michx.). Western thimbleberry (*Rubus parviflorus* Nutt.), baldhip rose (*Rosa gymnocarpa* Nutt.), and Utah honeysuckle (*Lonicera utahensis* Wats.) are common shrubs. Study 1 was located on the Palouse Ranger District of the Clearwater National Forest near Bovill, Idaho. Climate is subhumid to humid with a Mediterranean precipitation pattern of cool, dry summers and cool, wet winters. The study area's annual precipitation averages 90 cm (White 1985) and elevation is about 880 m. Soils are classified as medial over loamy, mixed, Andeptic Paleoboraefs (Dechert 1982).

Study 2 was conducted within the *Thuja plicata/Clintonia uniflora* (western redcedar/queencup beadlily) habitat type, the most common western redcedar habitat type in northern Idaho (Cooper et al. 1991). Western redcedar (*Thuja plicata* Donn.) dominates the potential natural community overstory with the seral tree species Douglas fir, grand fir, western white pine (*Pinus monticola* Dougl.), and western larch (*Larix occidentalis* Nutt.) also present. Common understory herbs and shrubs include queencup beadlily, sweetscented bedstraw, western goldthread (*Coptis occidentalis* (Nutt.) T. & G.), bunchberry dogwood (*Cornus canadensis* L.), and globe huckleberry (*Vaccinium globulare* Rydb.). Study 2 was located on the St. Maries Ranger District of the Idaho Panhandle National Forest near St. Maries, Idaho. The area's climate is similar to that of Study 1; average annual precipitation is about 75 cm (NOAA 1988) and elevation is about 870 m. Soils are fine-silty, mixed, Typic Fragiboralfs (Dechert 1982).

Methods

A total of 5 representative plant communities was selected within each habitat type. The size range of the 10 plant communities was 122 ha to 610 ha. Each community represented a different stage of succession: herb-shrub, sapling (trees 3–7 years old), pole (trees 8-15 years old), mature (trees >15 years old, 30–50% tree canopy cover), and potential natural community (80–90% tree canopy cover). Plant species composition, based on canopy cover $\leq$ 2.1 m above ground, was sampled within each of the 5 successional communities per habitat type. This height was selected because it is the maximum height from which elk can prehend forage (Patton and Hall 1966). The line intercept method (Canfield 1941) was used to estimate shrub and tree canopy cover by species along five 30.5-m transects per plant community. Herbaceous canopy cover by species was ocularly estimated within ten 1.0-m^2 quadrats placed at 3.1-m intervals along each transect.

Botanical composition of diets from free-ranging cattle, elk, and white-tailed deer was estimated using microhistological analysis of fecal samples (Sparks and Malechek 1968). In early summer (June 1), mid-summer (Aug. 15), and early fall (Oct. 15) of 1987 and 1988, 8 fresh fecal samples per animal species were randomly collected from within each type of successional plant community. An equal number of fecal samples was collected from each seral stage to ensure an unbiased sample. However, all 3 ungulates ranged freely throughout the study areas. The total area within Study 1 was about 64 km2 and about 57 km^2 in Study 2.

The 8 fecal samples from each animal species/plant community combination (8 samples × 3 ungulates × 5 plant communities × 3 seasons × 2 years = 720 total samples habitat type^{-1}) were composited before microhistological analysis (n = 90 habitat type^{-1}). Reference slides of the study area's flora were prepared and studied prior to fecal analysis. Fecal samples were analyzed by experienced technicians at Washington State University's Habitat Laboratory. Five microscope slides were prepared from each composite sample, with 25 fields of view examined from each slide at 100x magnification. A gridded lens eyepiece in the microscope was used to estimate the percentage cover of plant fragments.

Experimental design was completely randomized. Sampling within the successional plant communities was replicated in time (1987 and 1988), but within Study 1 and Study 2 the successional plant communities and ungulate herds were not replicated in space. Experiments that are not replicated in space are appropriate if the statistical inferences drawn are limited to the particular study site(s) (Wester 1992). However, inferences from Study 1 and Study 2 may be extended to other sites within the grand fir/queencup beadlily habitat type and the western redcedar/queencup beadlily habitat types, respectively. The habitat type classification system integrates the effects of environmental factors (e.g., soil, aspect, elevation, precipitation) on plant growth, reproduction, and competition (Daubenmire 1952, Hironaka et al. 1991).

Kulcyznski's similarity index (Oosting 1956, Olsen and Hansen 1977) was used to examine dietary overlap among the 3 ungulates. In this study, 2 diets were considered to be similar when the index was >50%. Dietary overlap data were subjected to analysis of variance with each ungulate species/season combination representing a treatment. Years were the replicates, pairwise comparisons were made using Fisher's Protected L.S.D. test (Steel and Torrie 1980), and significant differences were declared at $P \leq 0.10$. Kulcyznski's similarity index also was used to compare the botanical composition of the animal diets vs the botanical composition of the different successional plant communities. This enabled us to evaluate the degree of association between each ungulate and each seral stage. Indices of >50% similarity between an ungulate's diet and a specific successional community indicated that a notable portion of the ungulate's diet was harvested from within that particular seral stage. Similarity indices were subjected to analysis of variance in a 3 × 5 × 3 factorial arrangement; ungulate species, successional plant communities, and seasons were the factors and all were deemed random effects. Years were the replicates. Pairwise comparisons were made using Fisher's Protected L.S.D. test and significant differences were declared at $P \leq 0.10$. We also wanted to estimate the degree to which cattle, elk and white-tailed deer overlapped in their selection of foraging sites. This was accomplished by qualitatively comparing amongst the 3 ungulates the degrees of similarity between their diets and the botanical composition of each successional plant community.

Results

Study 1 (Grand Fir Habitat Type)

Graminoids were the dominant forage consumed by cattle in all 3 seasons, averaging 96% of the diet (Table 1). Kentucky bluegrass (*Poa pratensis* L.) and sedge (*Carex* spp. L.) were the dominant components. These also were the 2 plant species most consumed by elk. Graminoid consumption by elk was greatest in mid-summer, comprising 93% of the diet; graminoids averaged 59% and 55% of elk diets in early summer and early fall, respectively). Forb consumption by elk was highest in early fall while shrub consumption by elk was highest in early summer. Western goldthread was a notable forb and western serviceberry (*Amelanchier alnifolia* Nutt.) an important shrub in elk diets. White-tailed deer diets were generally more diverse (i.e., greater species richness) than cattle or elk diets. Graminoid consumption by white-tailed deer declined steadily as the growing season progressed, whereas forb consumption increased. Shrub consumption by white-tailed deer remained constant, averaging 42% across the 3 seasons. Globe huckleberry and western goldthread were important shrub and forb species, respectively. Conifers were a notable forage component in early summer and mid-summer.

Cattle and elk diets overlapped notably in all seasons, but especially in mid-summer when diets were 88% similar. Dietary overlap between cattle and white-tailed deer was ≤21% in all seasons, while overlap between elk and white-tailed deer was ≤34% in all but early summer (Table 2).

When we compared the botanical composition of the animal diets vs. the botanical composition of the 5 successional plant communities, there was a significant interaction between ungulate species and season (p=0.0478) and between ungulate species and successional plant community (p=0.0001). For cattle diets, overlap differed in all seasons (p=0.0003 in early summer; p=0.0009 in mid-summer; and p=0.0097 in early fall; Table 3). Cattle diets most closely matched herb-shrub communities in all seasons (42–51% similar). The botanical composition of cattle diets was somewhat similar (32–41%) to the botanical composition of sapling and pole stands. This indicates that much of the diet consumed by cattle was probably harvested from within herb-shrub communities, and to a lesser degree from sapling and pole communities. Cattle apparently harvested very little forage in the mature or potential natural communities. The degree of overlap between the botanical composition of elk diets and the seral plant communities differed in early summer (p=0.0981) and mid-summer (p=0.0001), but not in early fall (p=0.3853). Similar to cattle, in early summer and mid-summer the botanical composition of elk diets more closely resembled (34-52% similar) the botanical composition of earlier seral communities, but in early fall elk appeared to readily harvest forage from within all 5 seral stages. Overlap between white-tailed deer diets and seral plant communities differed in all 3 seasons (p=0.0005 in early summer; p=0.0011 in mid-summer; and p=0.0001 in early fall; Table 3). White-tailed deer diets were closely associated (47–61% similar) with the later seral stages (i.e., mature and potential natural community) in all seasons.

Study 2 (Western Redcedar Habitat Type)

Graminoids comprised most of the cattle diet in all seasons, averaging 92%. Kentucky bluegrass was the major plant species (Table 4). Elk in early summer consumed nearly equivalent proportions of graminoids, forbs, and shrubs, but elk diets became more dominated by graminoids as the growing season progressed. Kentucky bluegrass was the principal graminoid in the diet of elk in all 3 seasons, averaging 40% of the total diet. White-tailed deer also consumed nearly equivalent proportions of graminoids, forbs, and browse in early summer, but unlike elk, white-tailed deer decreased their graminoid consumption and increased their

Table 1. Mean (±SE) percentage botanical composition of cattle, elk, and white-tailed deer diets within a grand fir/queencup beadlily habitat type in northern Idaho.

	Cattle			Elk			White-Tailed Deer		
Forage	ES[1]	MS	EF	ES	MS	EF	ES	MS	EF
					%				
Graminoids									
Bromus vulgaris	——	——	——	——	——	——	——	1.6±1.2	——
Carex spp.	24.0±5.6	9.0±2.6	18.8±5.2	15.3±0.1	12.9±3.4	7.8±1.4	0.8±0.6	0.6±0.4	——
Dactylis glomerata	1.4±1.4	2.6±2.5	2.8±2.8	3.2±3.2	——	——	——	——	——
Deschampsia caespitosa	2.2±2.2	——	——	——	——	——	——	——	——
Festuca scabrella	1.9±1.9	7.4±1.6	5.9±0.4	——	8.2±2.2	3.1±0.7	3.1±2.1	——	——
Poa pratensis	51.6±7.8	68.3±2.3	53.2±4.7	35.2±4.9	65.3±9.1	40.6±14.4	7.4±2.0	2.8±1.9	——
Stipa occidentalis	6.6±2.4	——	——	——	——	——	——	——	——
Other	8.0±1.9	11.6±0.8	13.5±3.0	5.6±5.4	6.6±0.2	3.7±0.7	5.2±3.7	3.8±2.7	2.6±0.2
Total	95.6±0.0	98.9±0.0	94.3±3.6	59.3±7.1	93.0±3.3	55.2±14.4	16.5±11.1	8.8±0.8	2.6±0.2
Forbs									
Coptis occidentalis	——	——	——	——	——	15.8±2.8	——	——	11.6±1.0
Cornus canadensis	——	——	——	——	——	7.4±7.4	——	3.6±2.5	8.7±0.1
Fragaria vesca	——	——	——	——	——	——	——	1.8±1.2	6.4±1.4
Potentilla gracilis	——	——	——	——	——	——	——	2.5±1.8	——
Taraxacum officinale	——	——	——	——	——	——	——	2.0±1.4	——
Trifolium repens	——	——	——	——	——	——	——	2.4±1.6	1.6±1.2
Other	3.2±0.7	0.6±0.4	0.2±0.2	14.6±3.0	2.2±0.8	4.2±1.1	24.6±0.4	21.6±6.2	22.3±5.2
Total	3.2±0.7	0.6±0.4	0.2±0.2	14.6±3.0	2.2±0.8	27.4±11.4	24.6±0.4	35.5±7.4	50.6±6.5
Shrubs									
Amelanchier alnifolia	——	——	——	12.3±1.6	——	5.0±0.8	7.0±2.6	3.0±2.0	——
Pachistima myrsinites	——	——	——	——	——	——	——	8.0±4.2	9.0±1.8
Rosa gymnocarpa	——	——	——	——	——	——	——	2.8±1.9	——
Salix spp.	——	——	——	——	——	——	5.2±2.0	——	——
Spiraea betulifolia	——	——	——	——	——	——	5.5±0.6	——	——
Symphorocarpus albus	——	——	——	——	——	——	2.8±1.2	4.0±0.2	——
Vaccinium globulare	——	——	——	——	——	——	14.2±0.8	14.4±0.8	19.2±2.2
Other	0.4±0.4	——	4.0±2.5	11.4±3.8	2.0±0.2	7.4±2.8	8.5±0.8	11.4±2.4	10.7±3.9
Total	0.4±0.4	——	4.0±2.5	23.7±2.2	2.0±0.2	12.4±3.6	43.2±8.0	43.6±6.7	38.9±3.6
Conifers	0.4±0.4	0.2±0.2	0.4±0.4	1.4±1.4	2.4±2.4	3.8±0.4	12.3±4.2	8.5±2.6	3.1±0.5
Mosses/Lichens	0.2±0.2	0.2±0.1	1.0±0.4	1.0±0.5	0.4±0.1	1.2±0.1	3.4±1.6	3.6±0.7	4.8±2.6

[1] ES = early summer, MS = mid-summer, EF = early fall.

browse consumption as the growing season advanced. Western serviceberry averaged 8% of white-tailed deer diets across all 3 seasons. Willow (*Salix* spp. L.) averaged 10% of white-tailed deer diets in early summer and mid-summer, and globe huckleberry was notable (32% of diet) in early fall.

Dietary overlap between cattle and elk was small (37% similarity) in early summer, moderate (53% similarity) in mid-summer, and fairly high (74% similarity) in early fall (Table 5). Cattle diets in early summer averaged 56% similarity with elk diets in mid-summer and early fall. There was very low dietary overlap (≤31%) between cattle and white-tailed deer in all seasons. In contrast, sizable dietary overlap (57%) existed between elk and white-tailed deer in early summer, and elk diets in early summer were also very similar (60%) to white-tailed deer diets in mid-summer.

The comparison of the botanical composition of the animals' diets to the botanical composition present in the 5 successional plant communities found a significant (p=0.0014) 3-way interaction between ungulate species, season, and successional plant community. For cattle diets, overlap differed throughout the growing season (p=0.0097 in early summer; p=0.0060 in mid-summer; and p=0.0290 in early fall; Table 6). Cattle diets more closely resembled the earlier seral stages. This suggests that most of the forage ingested by cattle was harvested from plant communities in the herb-shrub, sapling, and pole stages of succession. In contrast, the degree of overlap between the botanical composition of elk diets and seral plant communities differed in early fall (p=0.0011) but not in early summer (p=0.6830) or mid-summer (p=0.1483). Elk diets in early fall more closely resembled the earlier successional stages. Overlap between the botanical composition of white-tailed deer diets and seral plant communities (Table 6) differed in mid-summer (p=0.0040) and early fall (p=0.0034), but not in early summer (p=0.3174). White-tailed deer diets in mid-summer and early fall were more similar in botanical compositon to later successional stages.

Discussion and Conclusions

Diet selection by free-ranging ungulates is influenced by many plant and animal factors. Plant factors include phenology, morphology, height, and species composition (Marten 1978). Animal factors include age, sex, physiological status, previous experience, and digestive anatomy. Weather can also influence diet selection (Arnold and Dudzinski 1978). But when all of these factors are held constant amongst 3 different species of ungulates, as was the situation in our study, the overriding determinant of diet selection is animal body size (Hanley 1982, 1984). Therefore, it

Table 2. Mean (±SE) percentage dietary overlap between cattle, elk, and white-tailed deer within a grand fir/queencup beadlily habitat type in northern Idaho (LSD = 17.4 at α=0.10).

	Cattle			Elk			White-Tailed Deer		
	ES[1]	MS	EF	ES	MS	EF	ES	MS	EF
					%				
Cattle(ES)		72.6±12.6	79.4±11.0	57.8±7.4	74.1±12.5	51.9±7.0	15.6±5.9	11.4±0.4	7.0±0.2
Cattle (MS)			81.6±4.3	51.0±7.6	87.7±2.8	56.1±14.4	18.2±10.2	8.2±0.5	3.7±0.2
Cattle (EF)				60.4±12.2	79.9±6.9	56.4±13.8	21.2±14.2	12.8±3.1	8.3±3.8
Elk (ES)					57.1±2.8	62.2±1.4	45.8±0.3	30.8±4.6	29.0±7.2
Elk (MS)						61.2±11.8	18.3±2.7	13.6±3.4	8.9±2.5
Elk (EF)							33.6±3.1	23.8±4.1	34.4±7.4
Deer (ES)								62.4±1.4	49.4±4.4
Deer (MS)									65.0±3.2

[1] ES = early summer, MS = mid-summer, EF = early fall.

is not surprising that the botanical composition data from the diets of the 3 ungulates followed the conceptual relationship between animal body size and diet selection described by Hanley (1982). The smallest sized species (i.e., white-tailed deer) consumed a diverse, concentrate-feeder diet dominated by forbs and shrubs. Conversely, the largest sized species (i.e., cattle) consumed a less diverse, more roughage-dominated diet. Elk also ingested predominately roughage, but as a slightly smaller animal than cattle, elk exhibited a more diverse diet selection. Elk and white-tailed deer diets were generally more diverse in the redcedar habitat type than in the grand fir habitat type. This was likely attributable to smaller relative differences in palatability amongst plants within the more mesic redcedar habitat type.

Cattle diets in this study were comprised of less browse than those reported by Thilenius and Hungerford (1967). This discrepancy is probably due to the fact that cattle in the earlier study were confined within an enclosure with a dense tree canopy where graminoid availability would be limited.

Kentucky bluegrass and sedge were important forages for cattle and elk in both habitat types throughout the growing season. These two plants would be appropriate key species for monitoring cattle and elk grazing impacts. It is interesting to note that in the redcedar habitat type cattle selected timothy (*Phleum pratense* L.), a cool season perennial grass, but timothy was not ingested by either elk or white-tailed deer in the redcedar habitat type.

Diet selection by elk differed between the 2 habitat types. In the grand fir habitat type, elk selected diverse diets in early summer and early fall, but elk diets were almost solely comprised of graminoids in mid-summer. This contrasts with the redcedar habitat type where the proportion of forbs and shrubs in elk diets decreased as the season progressed and the proportion of graminoids concomitantly increased. The reason for this difference in elk diet selection between habitat types is not evident from the data we collected. Our results differ from Hash (1973) who found elk diets were dominated by graminoids in early summer and then were more diverse during mid-summer and early fall. The differing results are probably due to the different weather conditions encountered during the 2 studies. Hash's study occurred in 1972. That summer his study area received above average precipitation in August (NOAA 1972) which may have kept forbs and leaves of shrubs more abundant and more palatable later in the season. August and September precipitation was below normal during our study (NOAA 1987, 1988).

White-tailed deer diets were comprised of substantial amounts of graminoids in early summer but the graminoid proportion steadily decreased as the growing season progressed. We attribute this to decreasing relative palatability of the graminoids as they matured. Roberts (1956) and Shaw (1962) reported similar graminoid consumption patterns by white-tailed deer inhabiting coniferous forests of northern Idaho. White-tailed deer consumed more grass in the more mesic redcedar habitat type than they consumed in the grand fir habitat type, again presumably due to smaller relative differences in palatability between graminoids,

Table 3. Mean (±SE) percentage overlap between botanical composition of ungulate diets and successional plant communities within a grand fir/queencup beadlily habitat type in northern Idaho.

Plant	Cattle			Elk			White-Tailed Deer		
Community	ES[1]	MS	EF	ES	MS	EF	ES	MS	EF
					%				
Herb-Shrub	50.6±0.6a[2]	42.0±2.0a	47.0±0.3a	52.0±3.4a	46.8±3.6a	41.6±0.2a	9.2±3.3a	7.8±0.6a	1.2±0.6a
Sapling	38.1±2.8b	34.6±3.2b	32.4±9.7b	45.5±5.4ab	34.0±0.8b	35.2±0.2a	25.1±6.9b	22.8±0.6b	14.6±2.0b
Pole	36.0±0.0b	34.8±2.2b	40.9±7.3ab	44.7±3.0ab	35.0±0.7b	30.7±4.8a	26.8±2.4b	28.1±0.8b	23.9±0.0c
Mature	14.4±2.2c	14.8±0.4c	19.6±5.0c	34.0±2.8bc	13.4±1.2c	29.6±7.2a	49.7±4.2c	51.9±2.7c	61.2±0.6d
PNC[3]	8.1±0.4d	4.8±0.3d	9.5±3.4c	31.8±7.6c	8.7±1.0d	37.1±9.2a	46.6±2.3c	48.0±6.0c	57.4±2.0e

[1] ES = early summer, MS = mid-summer, EF = early fall.
[2] Means within a column followed by the same letter are not different (P>0.10).
[3] PNC = potential natural community.

Table 4. Mean (±SE) percentage botanical composition of cattle, elk, and white-tailed deer diets within a western redcedar/queencup beadlily habitat type in northern Idaho.

	Cattle			Elk			White-Tailed Deer		
Forage	ES[1]	MS	EF	ES	MS	EF	ES	MS	EF
	%								
Graminoids									
Agropyron spicatum	7.4±5.1	10.6±10.0	1.6±0.5	2.0±1.5	1.4±0.9	——	——	——	——
Agrostis stolonifera	10.0±8.4	2.8±2.0	2.7±0.4	——	——	——	——	——	——
Bromus vulgaris	7.6±2.6	6.6±1.8	8.8±6.0	2.2±1.6	——	2.4±1.7	——	——	——
Carex spp.	0.8±0.3	5.4±5.1	9.7±1.9	2.8±0.2	4.8±2.8	18.0±4.0	1.2±0.3	——	——
Phleum pratense	7.5±1.3	2.0±0.4	3.0±0.9	——	——	——	——	——	——
Poa pratensis	46.2±15.9	50.3±23.9	60.8±6.2	19.0±4.5	47.5±2.3	52.9±3.2	11.0±3.9	8.0±0.8	——
Other	13.4±2.0	13.2±4.0	4.5±2.2	7.0±4.4	9.6±3.8	6.6±0.6	13.9±0.6	7.0±0.3	1.9±0.2
Total	92.8±0.6	91.0±0.6	91.2±0.6	33.0±8.9	63.3±5.6	79.9±0.8	26.1±4.8	15.0±0.5	1.9±0.2
Forbs									
Coptis occidentalis	——	——	——	——	——	——	——	——	2.9±2.0
Cornus canadensis	——	——	——	——	——	——	——	2.6±1.8	2.0±1.5
Fragaria vesca	——	——	——	——	——	——	——	3.8±2.8	——
Trifolium repens	——	——	——	9.6±6.7	5.9±3.1	1.4±1.1	1.8±1.2	7.2±2.2	——
Other	3.1±0.5	5.4±0.6	1.7±1.6	27.0±1.6	10.4±2.2	7.7±0.4	35.1±5.3	33.7±2.6	22.6±11.4
Total	3.1±.05	5.4±0.6	1.7±1.6	36.6±8.0	16.3±5.2	9.1±1.0	36.9±3.6	47.3±6.0	27.5±6.5
Shrubs									
Amelanchier alnifolia	——	——	——	6.8±3.0	5.2±0.5	——	7.8±3.4	10.0±0.4	6.7±4.7
Pachistima myrsinites	——	——	——	2.2±1.6	3.6±2.5	——	——	——	——
Physocarpus malvaceus	——	——	——	——	——	——	2.1±1.5	——	——
Rosa gymnocarpa	——	——	——	2.2±1.6	——	——	1.6±1.2	——	——
Salix spp.	——	——	——	——	——	——	10.2±2.0	10.4±6.0	2.9±2.0
Symphorocarpus albus	——	——	——	2.6±1.8	——	——	——	3.4±2.4	——
Vaccinium globulare	——	——	——	3.0±2.1	——	——	4.4±2.1	——	32.4±16.3
Other	2.3±1.6	1.8±0.4	0.4±0.1	8.5±0.5	6.8±1.4	5.8±1.6	6.6±5.2	10.7±3.6	19.0±2.7
Total	2.3±1.6	1.8±0.4	0.4±0.1	25.3±1.4	15.6±4.4	5.8±1.6	32.7±4.9	34.5±6.1	61.0±4.0
Conifers	0.2±0.2	——	2.2±2.2	2.4±1.8	1.4±0.9	0.8±0.5	3.2±2.3	1.4±0.6	6.2±0.2
Mosses/Lichens	1.5±0.2	1.8±0.4	4.4±0.1	2.7±0.1	3.4±2.6	4.4±2.2	1.1±0.1	1.8±1.1	3.4±2.0

[1] ES = early summer, MS = mid-summer, EF = early fall.

forbs, and shrubs. This also likely explains why white-tailed deer in the redcedar habitat type appeared to forage more within the herb-shrub community of the redcedar habitat type than they did within the herb-shrub community of the drier grand fir habitat type. It is also noteworthy that graminoid consumption by white-tailed deer was more negatively influenced by advancing plant maturity than was graminoid consumption by elk. This result further supports the concept of smaller-sized animals needing to ingest diets of greater relative digestibility.

Cattle and elk had high dietary overlap (Table 2) and apparently foraged in similar places (Table 3) throughout the summer in the grand fir habitat type. This does not necessarily mean that the relationship between cattle and elk was competitive (i.e., direct interference or amensalism). As discussed earlier, all 5 forms of interspecific relationships remain plausible, even if 2 ungulate species have complete dietary and spatial overlap. Dietary and spatial overlap data merely provide circumstantial evidence about interspecific relationships. If forage competition was occurring between cattle and elk, it was probably focused on Kentucky bluegrass and sedge in the herb-shrub and sapling communities.

Table 5. Mean (±SE) percentage dietary overlap between cattle, elk, and white-tailed deer within a western redcedar/queencup beadlily habitat type in northern Idaho (LSD = 19.6 at $\alpha = 0.10$).

	Cattle			Elk			White-Tailed Deer		
	ES[1]	MS	EF	ES	MS	EF	ES	MS	EF
	%								
Cattle (ES)		80.4±4.4	68.4±10.8	37.0±8.8	54.6±13.0	57.0±9.0	29.6±2.6	21.8±0.8	8.8±1.0
Cattle (MS)			71.1±11.3	38.8±12.5	53.4±10.2	61.4±4.4	31.1±0.4	23.2±0.8	10.8±0.3
Cattle (EF)				34.0±5.5	63.4±4.6	74.3±5.1	20.0±4.4	17.4±1.2	9.2±2.2
Elk (ES)					55.7±5.4	45.6±8.6	57.4±4.6	60.0±1.4	39.4±4.8
Elk (MS)						77.0±3.2	44.2±0.6	44.4±3.8	26.0±2.0
Elk (EF)							32.7±0.5	31.2±0.6	19.5±0.5
Deer (ES)								70.6±5.2	46.0±28.2
Deer (MS)									46.6±19.6

[1] ES = early summer, MS = mid-summer, EF = early fall.

Table 6. Mean (±SE) percentage overlap between botanical composition of ungulate diets and successional plant communities within a western redcedar/queencup beadlily habitat type in northern Idaho.

	Cattle			Elk			White-Tailed Deer		
	ES[1]	MS	EF	ES	MS	EF	ES	MS	EF
	%								
Herb-Shrub	44.2±7.4a[2]	35.2±5.0a	32.2±0.2a	51.0±7.6a	48.7±2.7a	42.4±1.6a	48.1±3.5a	39.2±0.4a	17.8±4.6a
Sapling	48.4±5.6a	41.2±7.8a	26.0±7.2a	45.2±8.0a	50.1±2.9a	43.2±1.6a	43.1±3.9a	34.1±0.3b	14.6±0.1a
Pole	38.1±2.5a	34.2±3.8a	31.8±2.5a	46.2±8.0a	47.9±3.2a	41.2±1.6a	38.6±1.2a	39.6±1.0a	15.5±0.3a
Mature	11.8±1.8b	13.1±1.2b	6.8±2.6b	47.8±6.6a	31.8±10.4a	20.4±1.4b	50.6±1.8a	55.6±0.8c	47.5±6.8b
PNC[3]	10.6±0.4b	12.2±0.5b	9.7±1.7b	49.0±1.2a	28.8±1.6a	19.5±1.5b	42.5±4.8a	49.4±3.4d	40.7±2.0b

[1] ES = early summer, MS = mid-summer, EF = early fall.
[2] Means within a column followed by the same letter are not different (P>0.10).
[3] PNC = potential natural community.

The probability of forage competition between cattle and elk was not as strong in the redcedar habitat type, except in early fall when the 2 ungulates appeared to both concentrate upon Kentucky bluegrass and sedge in the herb-shrub, sapling, and pole communities. Similar elk habitat use patterns were reported by Irwin and Peek (1983). Early successional plant communities would be appropriate key areas for monitoring grazing impacts by cattle and elk in both habitat types.

In both habitat types cattle and white-tailed deer exhibited low dietary overlap (Tables 2 and 5) and apparently did not forage much within the same successional plant communities (Tables 3 and 6). Thus, there is not much circumstantial evidence of forage competition between these 2 ungulates.

Elk and white-tailed deer in the grand fir habitat type overall had low dietary overlap (Table 2) and apparently foraged within different successional plant communities (Table 3). However, these 2 ungulates could potentially compete for western serviceberry in early summer and western goldthread in early fall. Other studies have also found western goldthread and western serviceberry to be important elk forages in summer (Hash 1973, Irwin 1978). In the redcedar habitat type, elk and white-tailed deer showed more circumstantial evidence of forage competition. In this habitat type elk and white-tailed deer in early summer had substantial dietary overlap (Table 5) and elk and white-tailed deer both appeared to forage readily within all 5 seral stages (Table 6). Elk diets in early summer also overlapped with white-tailed deer diets in mid-summer indicating that forage utilization by elk in early summer may have reduced the amount of preferred forage available to white-tailed deer in mid-summer. However, it is also possible that the forage utilization by elk in early summer enhanced the palatability or accessibility of forage for white-tailed deer in mid-summer. Western serviceberry would likely be an appropriate key species for monitoring browsing impacts of elk and white-tailed deer in both habitat types. Summer elk use of western serviceberry also may influence white-tailed deer in winter because this shrub is an important winter forage for white-tailed deer in these forests (Keay and Peek 1980). Shrub utilization by elk and white-tailed deer in the later successional communities also may impact Shiras moose (*Alces alces shirasi*) due to the heavy dependence by moose upon these shrub habitats during winter (Pierce and Peek 1984).

The principle of competitive exclusion suggests that the coexistence of the 2 cervids may be facilitated if they partition forage resources, either by feeding on different types of forage (i.e., plant species, plant parts, or plant heights) or by feeding in different habitats (Hardin 1960). Rocky Mountain elk and white-tailed deer in our study did appear to partition forages along the sere in the grand fir habitat type, and to a lesser degree in the redcedar habitat type. Less forage partitioning in the redcedar habitat type may have resulted from having relatively less graminoid standing crop within earlier seral stages of the more mesic redcedar habitat type. That is, the more mesic conditions reduced the differences in botanical composition along the sere, giving the 2 cervids less opportunity to partition foraging sites. A similar situation was observed by Leslie et al. (1987) between Roosevelt elk and Columbian black-tailed deer in western hemlock forests that had not been logged.

In summary, we compared dietary overlap among free-ranging cattle, Rocky Mountain elk, and white-tailed deer in coniferous forests of northern Idaho. Consistent with our hypotheses, cattle and white-tailed deer in both habitat types displayed insignificant overlap in selection of bites and foraging sites. Also consistent with our hypotheses, in the grand fir habitat type cattle and elk generally consumed diets of similar botanical composition from similar seral communities, whereas elk and white-tailed deer did not exhibit much dietary or foraging site overlap in the grand fir habitat type. However, contrary to our hypotheses, cattle and elk in the redcedar habitat type displayed similar bite and foraging site selection only in autumn. Also contrary to our hypotheses, in the redcedar habitat type elk and white-tailed deer had notable dietary overlap in early summer and foraged in similar plant communities in early summer and late summer. In the more mesic redcedar habitat type, elk apparently foraged more as intermediate feeders rather than bulk feeders.

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