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Elk (*Cervus elaphus roosevelti*) Dietary Composition and Quality in the Mount St. Helens Blast Zone

Abstract

We compared diet composition and diet quality of elk using the Mount St. Helens "blast zone" in 1985 to elk populations in more forested areas in the Pacific Northwest. Fecal analysis indicated that elk at Mount St. Helens consumed more forbs during summer (46-65% density of fecal fragments), more grasses during fall (38-62%), less ferns (< 3%), and in some cases less browse (20-42%), than has been reported for most west coast elk populations. Early successional forbs such as fireweed (*Epilobium angustifolium*), pearly everlasting (*Anaphalis margaritacea*), catsear (*Hypochaeris radicata*), mesic community species such as horsetail equisetum (*Equisetum* spp.) and willow (*Salix* spp.), and pasture grasses such as red fescue (*Festuca rubra*) and ryegrasses (*Lolium* spp.) that were seeded after the eruption were dominant in the feces of Mount St. Helens elk. Levels of *in vitro* dry matter digestibility in the diets of Mount St. Helens elk were higher and crude protein equal or lower than in diets of elk inhabiting managed and old-growth forests elsewhere in the Pacific Northwest. We hypothesize that because of nutritional differences in diets, elk inhabiting primarily old-growth forests will have a lower mean fecundity and higher mortality rate than elk inhabiting managed forests at the same elk densities. However, because structural characteristics of old-growth forests buffer elk from high travel costs and reduced forage availability during periodic heavy, wet snows, we hypothesize that vital rates will be less variable.

Introduction

Large-scale conversion of old-growth forests to even-aged, regenerating forests has caused concern over the loss of old-growth forests to west coast cervid populations (Smithey *et al.* 1985, Raedeke and Lemkuhl 1985). Benefits of old-growth forests to deer (*Odocoileus hemionus*) and elk have been attributed to 3 forest characteristics: (1) overstory structure that intercepts a substantial amount of snow, yet has sufficient openings to let sunlight reach the forest floor and promote understory development (Bunnell and Jones 1984, Hanley and Rose 1987), (2) abundance of arboreal lichens as a source of forage (Stevenson and Rochelle 1984), and (3) value as thermal cover (Schoen *et al.* 1984, Zahn 1985). The importance of old-growth forest characteristics to cervid species varies seasonally and across geographic areas depending on climatic regimes and characteristics of other habitats (Hanley *et al.* 1984). Where snow accumulates in winter, as in southeast Alaska, deer may require old-growth forests for energy conservation and foraging areas (Bunnell and Jones 1984, Hanley

1984). Further south, where snow is less persistent, a wider array of silvicultural options may exist for maintaining or enhancing cervid populations.

Understanding constraints on elk foraging behavior (Merrill 1994), and the nutritional adequacy of diets obtained from different forest types and seral stages are important prerequisites for evaluating management options for cervids. Elk in west coast forests show a high degree of dietary plasticity (Jenkins and Starkey 1991), which may affect nutrition and population dynamics. Diet composition and quality of elk populations have been examined in old-growth forests (Leslie *et al.* 1984, Leslie *et al.* 1987) and managed forests where several seral stages existed in proximity (Hanley 1984, Janz 1983). In this paper, we describe summer-fall composition and quality of diets of elk which inhabited the early successional forests that developed after the eruption of Mount St. Helens, and compare them to similar dietary studies on elk inhabiting later stages of forest succession in the Pacific Northwest.

Study Area

In 1985, we studied diet composition of elk inhabiting the northwestern portion of the Mount St. Helens "blast zone" in southwestern Washington within the Green River and North Fork of the Toutle River drainages. Elk reinvaded this area shortly

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after the eruption in 1980 and by 1985 helicopter surveys indicated summer elk densities were $1.8 \pm 0.20/\text{km}^2$ ($x \pm \text{s.e.}$) (Merrill 1987).

The Mount St. Helens area is included in the western hemlock (*Tsuga heterophylla*) zone (Franklin and Dyness 1973), although tree plantations prior to the eruption and adjacent to the blast zone were predominantly Douglas-fir (*Pseudotsuga menziesii*). Vegetative response in the 60,000 ha blast zone varied across the landscape depending on type of disturbance (e.g. pyroclastic flow, mudflow, blow-down, scorched), pre-eruption stand age, the presence of snow at the time of eruption, depth of tephra deposition, and post-eruption treatments (e.g. seeding, tree salvage operations, burning, bulldozing) (Mcans *et al.* 1982, papers in Bilderback 1987, Halpern *et al.* 1990). Because ash accumulation was relatively low, and salvage logging and site preparation mixed ash and soils, vegetation recovery in the northwestern portion of the blast zone was rapid.

Five early successional plant communities were identified based on species canopy coverage (Merrill 1987). The fireweed/pearly everlasting community made up the largest part of the study area (45%) and was dominated by catsear, groundsel (*Senecio sylvaticus*, *S. jacobaea*), thistle (*Cirsium arvense*), velvet grass (*Holcus lanatus*), blackberries (*Rubus ursinus*, *R. spectabilis*), and mahonia (*Berberis nervosa*). The fireweed/ glacier lily (*Erythronium grandiflorum*) community (4%) occurred at high elevations where ash accumulation was generally > 12 cm. Many of the same species occurred in this community as in the fireweed/pearly everlasting community, but canopy coverage was not as great, and several mesic-site species such as huckleberry, (*Vaccinium membranaceum*), dogwood (*Cornus canadensis*), and glacier lily were relatively abundant. The fireweed/red fescue community (20%) dominated sites that were young clearcuts (< 2 yrs) prior to the eruption and were aerially seeded after the eruption with a grass-clover mixture (e.g. *Lolium perenne*, *L. multiflorum*, *Festuca rubra*, *Trifolium pratense*, *T. repens*). The red fescue/clover (*Trifolium* spp.) community (14%) occurred only on the western portion of the debris avalanche of the North Fork Toutle River. Wet seep areas ($< 1\%$) were dominated by horsetail equisetum, rushes (*Juncus* spp.), montia (*Montia siberica*), and willow and were scattered throughout the study area. Forests adjacent to the blast zone (16%) were owned primarily by the

Weyerhaeuser Company. Douglas-fir was the primary tree species grown and site productivity was moderately high (Stevens *et al.* 1987).

Topography of the area is mountainous with elevations ranging from 240 m to about 1200 m. The climate is Pacific maritime with wet, mild winters and cool, dry summers. Annual precipitation is 225 cm/yr, occurring predominantly from November to April. Mean daily temperatures averaged 23°C in July.

Methods

Food habits of elk were determined using micro-histological identification of plant fragments in the feces of elk. Fresh fecal pellets were collected at elk feeding sites across the study area in June through November 1985. Five pellets from each of 50 groups were composited by month except for November when only 34 pellet groups were collected. Pellets were dried at 50°C for 48 hours. Each composite sample was ground and mixed in a Wiley mill to pass through a 0.1 mm screen.

Twenty slides of fecal plant fragments were prepared for each monthly fecal sample and 20 fields of view were read per slide. The amount each food item contributed to a sample (slide) was quantified using the frequency of occurrence of the species (Sparks and Malechek 1968). Frequencies were then converted to density estimates (Fracker and Brischle 1944).

Herbaceous plants comprising > 1 percent of the feces were collected and analyzed for percent nitrogen and *in vitro* digestibility when plants were in three phenological growth stages. Forbs were collected when they were vegetative, late vegetative-early flowering, and fruiting/mature. Grasses were collected when they were vegetative, flowering/fruiting, and senescent/cured. Species collections were made from at least 5 different plants at 5 sites and plant material combined. Only up to the terminal 10 cm of a plant was collected and plant parts were collected in the proportion they occurred on the terminal portion of a plant.

To approximate the nutritive value of herbaceous species eaten by elk each month, we used the value of the modal phenological stage of each species monitored at 10 sites. Two of the sites were at high elevation (> 900 m) and 8 at low elevation (≤ 900 m), which corresponded to the approximate distribution of observations of radio-collared elk (82% < 900 m, $n = 15$ elk) during the summer of 1984

(Merrill 1987). Predominate phenological stage at each site was determined by visually inspecting up to 50 arbitrarily chosen plants of each species. When we did not collect species eaten by elk at the modal phenology for nutritive analysis ($n = 15$ during the 6 months), and for unknown species within a forage category, we used the average nutrient value of all species in a forage class for the month.

Browse species were collected in early July to represent nutritive values of browse species in June and July, and in late August-early September to represent nutritive values in August and September. Composited shrub collections consisted of up to 10 cm of the terminal new growth of at least 20 different individuals of the major shrub species from 4 different sites. Leaves and stems were collected in proportion to their occurrence. In contrast, only new growth of twigs was collected in late October to represent nutritive values of browse in October and November because leaf drop was almost complete by mid-October.

All plants were dried at 50°C for 48 hours. Forage species were analyzed for nitrogen (N) using macro-kjeldahl techniques and for *in vitro* dry matter digestibility (IVDMD) following methods of Tilley and Terry (1963). A ruminally fistulated elk maintained on an alfalfa diet was used as the source of inoculum for IVDMD determinations.

The quality of a monthly diet was simulated following the procedure presented by Westoby (1974) and used by Leslie *et al.* (1984) and Janz (1983). Diet quality was the average monthly nutrient content of forages weighted by the proportion a forage occurred in the feces.

Differences in monthly fecal composition were compared by forage class using Tukey's HSD multiple comparison test. Percentage values were transformed using an arcsine-square root transformation prior to analysis (Sokal and Rohlf 1981). Seasonal trends in diet quality were examined using a Spearman rank correlation (r_s) (Siegel 1956). Differences in nitrogen and IVDMD between phenological stages were tested using paired t-tests by species within a forage class.

Results

Fecal Analysis

Forbs were dominant in the feces of elk from June through August, but declined in importance from September through November (Table 1). Five

forb species, including horsetail equisetum, catsear, pearly everlasting, fireweed, and clover, comprised 47-75 percent of the forb component of feces during summer. Graminoids in the feces comprised >60 percent in November. Grass species that were acrially seeded after the eruption to prevent ash erosion and to control dust, including red fescue, tall fescue (*Festuca arundinacea*), and annual rye grasses, were the dominant grass species in the fall fecal samples. Shrub use peaked in September, but comprised >20 percent of feces during all months. Willows, elderberry (*Sambucus racemosa*, *S. cerulea*), salmonberry (*Rubus spectabilis*), and huckleberry (*Vaccinium* spp.) consistently made up the greatest proportion of the shrubs found in the feces each month. Ferns comprised a consistently low proportion of the fecal samples.

Forage and Diet Quality

Quality of simulated elk diets was highest early in the growing season and declined as the season progressed ($r_s = 1.0$, $n = 6$, $P = 0.01$) (Table 2). By June, many grasses were already in flowering stage and had declined in forage quality. In contrast, most forbs consumed by elk in June were still in early stages of plant growth. IVDMD declined significantly in forbs and grasses with plant maturity (Table 3). Nitrogen declined rapidly in grasses and forbs between the vegetative stage and flowering stage (Table 3), but, thereafter, N decline in forbs was not significant ($t = 2.39$, $df = 4$, $P = 0.08$). Fern and conifer species were generally lower in IVDMD and N than other forage classes (Table 4). Nutritive values of shrubs declined significantly from summer to fall, but were high in N in fall compared to cured grasses.

Discussion

Mount St. Helens elk consumed more forbs during summer, more grasses during fall, less ferns, and in some cases less browse, than has been reported for most west coast elk populations (see Jenkins and Starkey 1991 for review). Differences in food habits among elk populations are probably due to broad-scale differences in the availability of different forage classes, since availability of forage classes (herbs, ferns, shrubs, conifers) is a predictable function of forest succession (Issac 1940, Long and Turner 1975, Harestad 1979, Witmer *et al.* 1985). Diets of elk at Mount St. Helens were dominated by forbs in summer and grasses in fall. Greater

TABLE 1. Mean percent density of plant fragments identified in elk feces collected in the northwestern portion of the Mount St. Helens blast zone during summer and fall of 1985.

	June	July	Aug	Sept	Oct	Nov
GRAMINOIDS						
<i>Agrostis</i> spp.	2.4	0.5	0.3	0.6	2.2	2.2
<i>Bromus</i> spp.	0.1	0.0	0.1	0.2	0.4	2.1
<i>Carex</i> spp.	2.2	1.6	0.4	0.5	0.7	1.6
<i>Dactylis glomerata</i>	0.1	0.5	0.3	0.3	2.4	4.3
<i>Deschampsia elongata</i>	0.7	0.0	0.3	0.6	1.3	1.1
<i>Elymus glaucus</i>	1.3	0.7	1.6	2.0	3.5	3.0
<i>Festuca arundinacea</i>	0.5	0.3	0.8	2.2	3.4	8.0
<i>Festuca rubra</i>	2.2	0.9	2.4	5.9	5.8	18.4
<i>Holcus lanatus</i>	2.0	1.2	2.0	2.2	3.8	5.1
<i>Juncus</i> spp.	0.8	0.8	0.1	0.2	0.5	0.4
<i>Lolium</i> spp.	1.5	0.2	0.2	1.8	6.0	6.7
<i>Luzula divaricata</i>	0.1	0.2	0.3	1.5	0.8	0.4
<i>Phleum pratense</i>	0.2	0.3	0.4	0.9	1.4	3.4
<i>Poa</i> spp.	0.1	0.1	0.8	0.8	1.5	0.4
Unidentifiable grasses	3.3	1.7	2.8	6.1	4.6	5.2
Total graminoids	17.5b	8.8a	12.8ab	25.8c	38.3d	62.3e
FERNS						
<i>Blechnum spicant</i>	1.2	0.2	0.2	0.0	0.2	0.6
<i>Lycopodium</i> sp.	0.1	0.1	0.1	0.0	0.3	0.1
<i>Polystichum munitum</i>	0.0	0.4	0.2	0.2	0.1	1.0
<i>Pteridium aquilinum</i>	1.3	0.8	0.0	0.2	0.3	0.6
Total ferns	2.6b	1.5ab	0.5a	0.4a	0.9a	2.3ab
FORBS						
<i>Achillea millefolia</i>	0.8	0.2	0.1	0.0	0.1	0.0
<i>Anaphalis margaritacea</i>	1.5	5.0	3.1	1.1	0.1	0.2
<i>Aranus sylvester</i>	0.1	0.0	0.0	0.0	0.0	0.0
<i>Dicentra formosa</i>	0.2	3.4	0.3	0.2	0.1	0.0
<i>Epilobium angustifolium</i>	0.2	8.2	28.5	4.2	4.5	1.2
<i>Epilobium glaberrimum</i>	1.0	2.7	0.5	0.0	0.0	0.0
<i>Equisetum</i> spp.	10.5	10.7	8.2	5.0	3.0	2.3
<i>Galium boreale</i>	0.1	0.0	0.0	0.0	0.0	0.0
<i>Hieracium albiflora</i>	0.1	0.1	0.0	0.0	0.0	0.0
<i>Hypochaeris radicata</i>	8.3	13.1	3.6	1.8	2.4	0.9
<i>Lotus corniculatus</i>	0.0	0.7	0.4	0.5	0.1	0.3
<i>Lysichitum americana</i>	0.2	0.0	0.1	0.0	0.0	0.0
<i>Lupinus</i> spp.	1.0	0.2	0.1	1.3	1.5	1.3
<i>Maianthemum dilatatum</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Mimulus guttatus</i>	0.8	0.4	0.5	0.1	0.0	0.0
<i>Montia siberica</i>	0.0	0.8	0.1	0.1	0.1	0.0
<i>Oxalis oregana</i>	0.3	0.1	0.0	0.0	1.6	0.6
<i>Plantago lanceolata</i>	0.3	0.2	0.0	0.0	0.0	0.1

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Table 1, continued

	June	July	Aug	Sept	Oct	Nov
<i>Petasites frigidus</i>	0.0	0.0	0.0	0.2	0.0	0.0
<i>Ranunculus radicata</i>	0.5	0.1	0.0	0.0	0.0	0.0
<i>Stachys cooleyae</i>	0.0	1.1	0.3	0.0	0.0	0.1
<i>Trifolium</i> spp.	4.6	2.5	3.3	7.1	4.0	2.5
<i>Typha latifolia</i>	0.1	1.3	0.7	0.5	0.0	0.0
<i>Veronica officinale</i>	0.2	0.1	0.0	0.0	0.0	0.2
Unidentifiable forbs	15.4	14.6	12.2	9.6	6.1	5.3
Total forbs	46.2c	65.5d	62.1d	31.7b	23.6b	15.0a
SHRUBS AND TREES						
<i>Acer circinatum</i>	1.9	0.0	0.3	0.7	0.2	0.8
<i>Acer macrophyllum</i>	0.9	0.4	0.7	0.6	0.2	0.3
<i>Alnus rubra</i>	0.7	0.2	0.1	0.9	0.6	0.1
<i>Berberis nervosa</i>	0.3	0.1	0.0	0.2	0.1	0.1
<i>Gaultheria shallon</i>	0.1	0.2	0.5	0.9	1.0	0.2
<i>Populus trichocarpa</i>	0.1	0.6	0.6	0.6	1.2	0.9
<i>Pseudotsuga menziesii</i>	2.0	0.0	0.1	0.2	0.1	0.1
<i>Ribes bracteosum</i>	0.0	0.1	0.0	0.0	0.0	0.0
<i>Rosa nutkana</i>	0.5	0.3	0.2	0.9	0.9	0.1
<i>Rubus ideaus</i>	0.9	0.3	0.1	0.6	0.1	0.0
<i>Rubus parviflorus</i>	0.1	0.1	0.4	0.2	1.2	0.8
<i>Rubus spectabilis</i>	3.1	1.2	1.3	3.4	2.3	0.9
<i>Rubus ursinus</i>	0.5	0.0	0.0	0.5	0.6	0.1
<i>Salix</i> spp.	15.6	15.1	14.0	21.5	18.1	5.8
<i>Sambucus racemosa</i>	1.5	2.1	1.4	2.1	2.2	1.8
<i>Tsuga heterophylla</i>	0.2	0.1	0.1	0.0	0.1	0.0
<i>Vaccinium</i> spp.	0.8	0.0	0.4	1.7	1.4	0.7
Unidentifiable shrubs	4.5	3.4	4.4	7.1	6.9	7.4
Total shrubs and trees	33.7bc	24.2ab	24.6ab	42.1c	37.2bc	20.4a
TOTAL	100	100	100	100	100	100

TABLE 2. Dietary levels of *in vitro* dry matter digestibility (%) and crude protein (% nitrogen x 6.25) for elk in the Mount St. Helens blast zone during the summer and fall of 1985.

Month	Digestibility	Crude Protein
June	61.8	15.6
July	57.8	14.7
August	52.2	12.3
September	47.2	9.8
October	45.5	8.9
November	44.2	7.1

than 85 percent of the composite home range of elk at Mount St. Helens was in early seral stages of forest succession. Standing herbaceous biomass averaged 1145 kg/ha in July in the early successional communities with forbs, grasses, and ferns comprising 63 percent, 26 percent, and 11 percent of the standing biomass, respectively (Merrill 1987). Grasses seeded after the eruption were conspicuous in about 34 percent of the composite home range of elk (20% on the debris avalanche which elk used only in fall and winter), while the remaining early successional communities (45%) could not

TABLE 3. Percent *in vitro* dry matter digestibility (IVDMD) and percent nitrogen (N) of major herbaceous forages collected by phenological stage from seral communities in the northwestern portion of the Mount St. Helens blast zone during the summer and fall of 1985.

	Vegetative		Flowering		Mature	
	IVDMD	N	IVDMD	N	IVDMD	N
GRAMINOIDS						
<i>Agrostis</i> spp.			58.3	1.34	35.9	0.54
<i>Carex</i> spp.	75.4	2.60	63.3	1.94	30.7	0.75
<i>Dactylis glomerata</i>	71.3	3.37	41.6	1.19		
<i>Deschampsia elongata</i>			58.8		36.1	
<i>Elymus glaucus</i>	71.1	3.75	64.8	1.40	46.9	0.84
<i>Festuca arundinaceae</i>	75.2	1.46	55.2	1.60	42.3	0.61
<i>Festuca rubra</i>	63.5	2.33	51.5	1.17	28.0	1.05
<i>Holcus lanatus</i>	80.8	2.56	64.9	2.18	53.7	1.65
<i>Lolium perenne</i>			62.3	1.09	39.9	0.76
<i>Luzula divaricata</i>			39.0	1.15	39.8	1.03
<i>Phleum pratense</i>			74.5	1.85		
<i>Poa</i> sp.			55.7	1.75	53.2	1.09
Mean ¹	72.8 ^a	2.63 ^a	57.5 ^b	1.52 ^a	40.7 ^c	0.92 ^c
FORBS						
<i>Anaphalis margaritacea</i>	68.5	2.57	57.3	2.32	43.3	1.79
<i>Dicentra formosa</i>			66.8	2.98		
<i>Epilobium angustifolium</i>	60.0	4.10	57.5	2.48	43.4	1.13
<i>Epilobium glaberrimum</i>	62.4	3.74	44.8	2.42	34.4	1.68
<i>Equisetum</i> spp.	65.5	2.28	50.7	1.43		
<i>Hypochaeris radicata</i>	75.0	1.77	69.4	1.63	63.9	1.30
<i>Lupinus</i> spp.	81.1	3.30	73.8	2.86	58.3	2.32
<i>Maianthemum dilatatum</i>	71.0					
<i>Mimulus guttatus</i>	73.6					
<i>Oxalis oregana</i>	86.9	2.06				
<i>Plantago lanceolata</i>	61.2		52.4	1.51		
<i>Ranunculus radicata</i>	66.8	2.75				
<i>Stachys cooleyae</i>	66.6		63.9	1.66		
<i>Trifolium</i> spp.	86.4	4.16	70.1	3.07	68.0	3.17
<i>Typha latifolia</i>	52.0	2.95	59.2	2.93		
<i>Veronica officinale</i>			62.1	1.78		
Mean	70.0 ^a	3.10 ^a	61.1 ^b	2.29 ^b	51.8 ^c	1.92 ^b

¹ Different superscripts indicate significant differences in IVDMD or N between phenological stages (vegetative vs. flowering, flowering vs. mature) within a forage class, paired t-test, $P \leq 0.05$.

be distinguished floristically from adjacent clear cuts outside the blast zone (Merrill 1987).

In contrast, analyses of elk feces collected in the Hoh Valley on the Olympic Peninsula of Washington (Leslie *et al.* 1984) indicated that elk diets were higher in ferns and conifers (23%) and lower in

forbs (37%) in summer, and lower in grasses in fall (17-26%) than elk feces at Mount St. Helens. Sixty-five percent of the composite home range used by elk in the Hoh Valley consisted of old-growth forests with understories dominated by swordfern, huckleberries, and mosses (Leslie *et al.* 1984). Early

TABLE 4. Percent *in vitro* dry matter digestibility (IVDMD), and percent nitrogen content (N) of up to the terminal 10 cm of new twigs and leaves of ferns and shrubs collected in early July and late August–early September, and of new twigs collected in late October in 1985 in the northwestern portion of the Mount St. Helens blast zone.

	July		September		October	
	IVDMD	N	IVDMD	N	IVDMD	N
FERNS						
<i>Blechnum spicant</i>	31.8	1.20	24.4	1.56	29.9	1.43
<i>Polystichum munitum</i>	26.2	3.38	20.7	2.22	20.0	1.55
<i>Pteridium aquilinum</i>	42.3	3.27	21.6	1.72	16.1	1.83
Mean	33.4	2.62	22.2	1.83	22.0	1.60
SHRUBS						
<i>Acer circinatum</i>	63.7	1.56	49.5	1.33	26.5 ¹	1.21
<i>Acer macrophyllum</i>	50.1	1.78	40.8			
<i>Alnus rubra</i>	49.6	2.70	37.2			
<i>Berberis nervosa</i>	64.7	1.83	38.9	1.10		
<i>Gaultheria shallon</i>	21.8	0.90	22.4	0.78		
<i>Populus trichocarpa</i>	60.2	3.19	56.1	1.68		
<i>Rubus idaeus</i>	44.8	2.24	46.9	1.72		
<i>Rubus parviflorus</i>	54.2	1.60	49.4	1.45	41.0	1.31
<i>Rubus spectabilis</i>	48.5	3.03	21.8	1.63	20.5	1.33
<i>Rubus ursinus</i>	54.0	1.78	40.2	1.53		
<i>Salix</i> spp.	46.5	2.83	34.1	1.60	27.7	1.61
<i>Sambucus racemosa</i>	68.3	3.01	58.6	1.92	48.0	1.20
<i>Vaccinium</i> spp.	58.7	2.90	48.7	1.80	39.9	1.38
Mean	52.7 ^a	2.25 ^{a 1}	41.9 ^b	1.50 ^b	33.9 ^c	1.34 ^c
CONIFERS						
<i>Pseudotsuga menziesii</i>	34.2	1.60	32.5	1.50	31.3	1.51
<i>Tsuga heterophylla</i>	30.3	1.30	27.0	1.36	25.7	1.33
Mean	32.3	1.45	29.8	1.43	28.5	1.40

¹ Different superscripts indicate significant differences in IVDMD or N between collection dates (July vs. September, September vs. October) within a forage class. paired t-test, $P \leq 0.05$.

successional forests were comparatively rare and grasses and forbs were primarily restricted to deciduous communities (e.g. big leaf maple, cottonwood, and alder communities) and areas along floodplains (Leslie *et al.* 1987). Both shrub abundance (4-47 kg/ha, Leslie 1983; Table 9) and the occurrence of shrubs (9%) in elk feces (Leslie *et al.* 1984) were low in the Hoh Valley. Heavy browsing by a high density, un hunted elk population have been reported for this area (Schwartz and Mitchell 1945, Jenkins and Starkey 1980, Leslie *et al.* 1987).

In managed forests of Vancouver Is., B.C. and western Oregon and Washington, where early and late successional stages were interspersed, fecal analysis indicated that diets of elk were also lower

in forbs (2-38%) in summer and grasses (4-38%) in fall than in elk diets at Mount St. Helens, but higher in shrubs (25-60%) (Janz 1983, Hanley 1984).

Fecal analysis presented here represent food consumed during only one summer and annual variation in diets is likely to occur. However, preliminary analysis of elk feces collected in the same area in May (grasses: 25%; forbs: 53%; shrubs: 15%; ferns: 4%; conifers: 3%) and November (grasses: 73%; forbs: 16%; shrubs: 6%; ferns: 4%; conifers: 1%) of 1982 (Merrill, unpublished data) indicated that the patterns we observed in 1985 were consistent among years. Snow was ephemeral in the 5 years following the eruption at the elevations where

elk spent fall and winter at Mount St. Helens and was not considered important in habitat selection (Merrill 1987) or probably diet selection (Merrill 1994).

Determination of diets from plant fragments in feces, also can be biased by differential digestibility of ingested plant species (Dcarden *et al.* 1975, Vavra and Holechek 1980, Holechek *et al.* 1982, Gill *et al.* 1983, Alipayo *et al.* 1992). Analyses of feces from elk inhabiting Mount St. Helens were not corrected for these potential biases, but based on corrections for common west coast species (Leslie *et al.* 1983) the high proportion of forbs and low proportion of ferns and conifers in the feces of Mount St. Helens elk are likely to reflect conservative trends in the diet.

Differences in food habits may have important implications for the quality of diets of west coast elk populations. Dry matter digestibility of simulated diets of elk at Mount St. Helens were about 30 percent higher in summer, and 25 percent higher in fall than has been reported for elk inhabiting old-growth forests in Olympic National Park, Washington (summer 41%, fall 37-40%; Leslie *et al.* 1984) and elk inhabiting managed forests on Vancouver Island, B.C. (summer 42%, fall 35%; Janz 1983). Differences were largely due to the high proportion of forbs consumed by elk at Mount St. Helens. Forbs, relative to evergreen ferns and conifers are high in IVDMD (Rochelle 1980, Leslie *et al.* 1984, Janz 1983, this study). Additionally, because cell walls of forbs are thin, they can be broken down and passed rapidly (Spalinger *et al.* 1986), thus permitting high total intake.

In contrast to IVDMD, crude protein levels of simulated elk diets at Mount St. Helens appeared to be equal or below those reported for other west coast areas (Leslie *et al.* 1984: summer 15.9%, fall 13.4%; Janz 1983: summer 15.3%, fall 9.9%). Particularly low levels of crude protein in simulated fall diets of Mount St. Helens elk were due to a high consumption of grasses (26 to 62%). Nonetheless, dietary crude protein in all studies exceeded the generally accepted 5-7 percent needed for meeting metabolic fecal losses (Mould and Robbins 1981), but were lower than the 20 percent needed for maximum weight gain by white-tailed deer fawns (Ullrey *et al.* 1967).

Because secondary plant compounds, such as tannins, reduce protein availability and digestibility of cell solubles, their concentrations may alter

the relative value of diet quality among areas. Only a few studies have quantified concentrations of tannins in west coast forages (Hanley *et al.* 1987, Happe *et al.* 1990, Hanley *et al.* 1992). If tannin levels are higher in forbs than other forage classes (Robbins *et al.* 1987a, Robbins *et al.* 1987b, Hanley *et al.* 1992), particularly when growing in the open (Hanley *et al.* 1987), the potential energy and protein in the diets of Mount St. Helens elk may be much lower than our data indicate. However, salivary proteins of elk may be similar to deer and reduce the effects of tannins by forming soluble complexes which are stable throughout the digestive tract (McArthur *et al.* 1991).

The above comparisons of food habits and dietary quality are tentative because of the short-term nature of the studies (≤ 2 years) and because of differences in sampling procedures and other characteristics of the study areas. For example, although the Mount St. Helens, Hoh Valley, and Vancouver Island study sites fall primarily within the western hemlock bioclimatic zone, differences in soils and total rainfall (Hoh Valley $>$ Vancouver Island \geq Mount St. Helens) are likely to influence the relative abundance of specific habitat types, which differ in species composition and potential forage value (Nyberg and Janz 1990). Nonetheless, we believe the data are sufficient to hypothesize that summer-fall nutrition of elk varies with the dominant pattern of forest succession in a landscape. In landscapes of primarily early successional stages, forbs and deciduous browse species are abundant and provide high energy intake because they are high in cell solubles, and have rapid passage rates. In contrast, areas dominated by ferns, evergreen shrubs, and conifers, as found in old-growth forests, may provide low energy intake, but adequate protein.

In fall, and in winter (Jenkins and Starkey 1993), availability of grasses to west coast elk can provide an important source of energy. Graminoids are typically more abundant in early seral communities than in closed canopied and old-growth forests (Harestad 1979, Hanley 1984, Leslie 1983, Merrill 1987). High standing crops of grasses, however, are limited primarily to disturbed sites, such as flood plains (Jenkins and Starkey 1980, Leslie *et al.* 1984), lowland wet meadows (Paige 1990), and seeded clearcuts (Becker 1989), since most natural grasslands in the west coast have been encroached by human settlement (Raedeke and Taber 1982).

Our arguments do not negate the importance of old-growth forests to elk in west coast environments. Instead, we hypothesize that elk populations living within landscapes dominated by different forest stages may have different population responses to environmental conditions as a result of distinctive nutritional regimes. If elk populations inhabiting primarily old-growth forests are more energy-limited relative to elk populations in naturally diverse or managed forests, particularly where grass seeding is a common practice, we hypothesize that they will have lower mean fecundity and higher mortality rates at the same elk densities. However, we hypothesize that these rates will be less variable than in managed forests because structural characteristics of old-growth forests buffer elk from high costs of travel and from reduced forage availability during periodic heavy, wet snows in winter. The limited

data available on long-term dynamics of elk populations in pastures and forests systems in western Oregon are consistent with these hypotheses (Taylor 1986). We encourage future studies to address the effects of forest dominance and diversity on population processes of elk.

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