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Effects of spotted knapweed on a cervid winter-spring range in Idaho

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Abstract

Spotted knapweed (*Centaurea maculosa* Lam.), an exotic member of the Compositae, infests large areas of rangeland in the northwestern United States. We assessed the impacts of infestation on a wilderness winter-spring range for elk (*Cervus elaphus nelsoni* Bailey), mule deer (*Odocoileus hemionus* Raf.), and white-tailed deer (*Odocoileus virginanus* Raf.) along the Selway River in Idaho and found no evidence of a large reduction in carrying capacity. We estimated cervid densities in open areas by scan sampling known area blocks. Densities in knapweed vegetation were greater than or equal to densities in areas of native bunchgrasses and sedges. Direct observation of animals and laboratory analyses of fecal and rumen samples showed spotted knapweed seedheads and rosette leaves were being eaten by all cervid species. Deer ate large amounts of rosette leaves at times in contrast to elk, which consumed them frequently, but in small amounts. Seedhead consumption was greatest during periods of snow cover. We collected composite samples of knapweed tissues and determined energy and protein content with standard laboratory techniques. Energy and protein content of rosettes was near that of preferred native food plants. Seedheads, while less nutritious than rosettes, remained easily obtainable above the snow. The amount of energy and protein available on sample plots decreased modestly at most after infestation. In composite samples of spotted knapweed the content of cnicin, a sesquiterpene lactone in aerial tissues, was determined by high performance liquid chromotography. Changes in cnicin levels did not appear to be responsible for seasonal changes in the amount of knapweed in cervid diets. When estimating or predicting carrying capacity of a cervid range, spotted knapweed should be considered a potential food.

Key Words: carrying capacity, spotted knapweed, *Centaurea maculosa*, elk, *Cervus elaphus*, mule deer, *Odocoileus hemionus*, white-tailed deer, *Odocoileus virginianus*, noxious plants

Resúmen

***Centaurea maculosa* Lam., un exótico miembro de las Compositae, invade grandes áreas de campo en el noroeste de los Estados Unidos. Se evaluó el impacto de invación en un área natural de invierno-primavera utilizada por *Cervus elaphus nelsoni* Bailey, *Odocoileus hemionus* Raf., y *Odocoielus virginanus* Raf. a lo largo del río Selway en Idaho y no se encontraron evidencias de una gran reducción en la capacidad de carga. Se estimó la densidad de cérvidos en áreas abiertas por "scan" observados en bloaos. La densidad de *C. maculosa* fue mayor o igual a la densidad de gramas agrupados y Cyperaceae. Observación directa de los animales y análisis, en el laboratorio, de fecas y muestras del rumen mostraron que las cabezas de semillas estaban siendo comidas por todas las especies de cérvidos. Los ciervos comieron grandes cantidades de hojas en roseta esporádicamente, en cotraste con *Cervus elaphus nelsonii*, el cual consumió estas frecuentemente pero en pequeñas cantidades. El consumo de las cabezas de semillas fue mayor durante períodos con cubierta de nieve. Se colectaron muestras compuestas de tejidos de *C. maculosa* y se determinó el contenido energético y proteico mediante técnicas estandar de laboratorio. El contenido energético y proteico de las rosetas fue cercano a aquellas plantas nativas comestibles preferidas. Las cabezas de semillas, si bien son menos nutritivas que las rosetas, permanecen fácilmente obtenibles por encima de la nieve. La cantidad de energía y proteína disponible en una muestra del terreno disminuyó modestamente, luego de la invasión. En las muestras compuestas de *C. maculosa* el contenido de *cnicin*, una lactona sesquiterpeno en tejidos aéreos, fue determinado por cromatografía líquida de alto funcionamiento. Los cambios en los niveles de *cnicin* no parecieron ser responsables por los cambios estacionales en la cantidad de *C. maculosa* en la dieta de los cérvidos. Al estimar o predecir la capacidad de carga en un campo utilizado por cérvidos, *C. maculosa* debería ser considerada un alimento potencial.**

Spotted knapweed (*Centaurea maculosa* Lam.) infests nearly 2 million ha in Idaho and Montana plus substantial and increasing areas in adjacent states and provinces (Roche 1988, Callihan and Sanders 1994). This Eurasian exotic, introduced to the Pacific Northwest around the turn of the century, is well adapted to soil types and climatic regimes common on cervid winter ranges in the region. On some ranges, like the Selway, it has become the dominant plant in open areas.

The value of spotted knapweed as a forage for wildlife and livestock was first thought to be minimal (Watson and Renney 1974, Strang et al. 1979). More recently it has been shown to have substantial nutritional value (Kelsey and Mihalovich 1987), and both domestic (Spoon et al. 1983, Cox 1983) and native grazers (Lavelle 1986, Miller 1990) eat portions of the plant.

The lower elevations (< 1525 m) of the Selway River drainage in central Idaho are an important winter-spring range for elk

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(*Cervus elaphus nelsoni* Bailey), mule deer (*Odocoileus hemionus* Raf.), and white-tailed deer (*Odocoileus virginianus* Raf.). Primary historical accounts such as journals, grazing allotment records, photographs, and interviews provide a history of the region since 1910. Large fires in the early 20th Century created conditions that encouraged a small, possibly indigenous elk population to expand to near-irruptive levels in the 1940's and 1950's. They remain the dominant grazers today. Cattle grazing ended by 1950, and grazing by pack and saddle stock has declined since the late 1960's. Neither had important impacts on vegetation except near scattered homesteads. Cheatgrass (*Bromus tectorum* L.) invaded many open ponderosa pine (*Pinus ponderosa* Dougl.)-bunchgrass sites as early as 1932, followed within a decade by goatweed (*Hypericum perforatum* L.) (Tisdale 1976). Spotted knapweed began gaining a foothold in dry bottomlands in the 1960's, and since has come to dominate much of the winter-spring range.

In this setting we collected data to meet several objectives: 1) to determine whether elk and deer densities in unforested sites dominated by spotted knapweed differed from densities in areas dominated by native vegetation, 2) to determine the amount of spotted knapweed eaten by elk and deer and their season of use, 3) to evaluate the nutritional quality of spotted knapweed and compare its energy and protein content to common well known food plants of elk and deer, 4) to estimate carrying capacity changes on sample plots after they became infested by knapweed, and 5) to compare seasonal changes in cnicin content of knapweed tissues with seasonal changes in the amount of these tissues included in cervid diets.

Study Area

Our 100-km^2 study area was located in the middle of the Selway River drainage in the Idaho portion of the Selway-Bitterroot Wilderness. It encompassed elevations from river level at 825 m up to 1,525 m, but only those areas within 6 km of the Selway River. The moist north slopes of the steep, dendritic drainages are heavily forested with Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) and grand fir (*Abies grandis* (Dougl.) Forbes). Xeric south and west exposures are dominated by spotted knapweed or other forbs. Bunchgrass/sedge (*Carex* spp. L.), brushfields dominated by serviceberry (*Amelanchier alnifolia* Nutt.), or open ponderosa pine forest grow on intermediate sites.

White-tailed deer and elk were abundant during all winter and spring months. Mule deer were abundant on the study area except during December. Adult bull elk were uncommon.

In a typical year, powder snow increases in depth from late-November through mid-January. Later in the winter crusting increases and snow cover decreases on south slopes. During March, snow cover disappears rapidly except on north slopes and at higher elevations. Maximum snow depths averaged 43 cm from 1967 through 1993 in the river bottom. Peak snow depths were 38 cm, 28 cm, 51 cm, 33 cm, 25 cm and 48 cm in 1991–1996 respectively (National Weather Service climatic data station maintained by ALW).

Methods

Cervid Densities

We estimated densities of cervids on spotted knapweed and bunchgrass/sedge vegetation types by observing them from 7 accessible view points throughout the study area. We mapped and computed the areas of knapweed and bunchgrass/sedge within 100–1,500 m of each point. We classified patches of vegetation as knapweed if we visually estimated > 75% of herbaceous cover was spotted knapweed. We classified vegetation as bunchgrass/sedge if > 50% of herbaceous cover was bunchgrass and sedge. Both vegetation types had less than 10% canopy cover over 2 m tall. Vegetation patches ranged from 3.9–22.3 ha for knapweed and from 2.4–5.0 ha for bunchgrass/sedge. Four of the 7 view points had both vegetation types present, and 3 had only knapweed. Because our objective was to identify sites that were either heavily infested or primarily native vegetation not to classify intermediate sites as being in one or the other category, we felt visual cover estimates and qualitative descriptions of sites were adequate.

Knapweed vegetation type—Sites meeting the criteria for this vegetation type occurred on moderately steep (30 to 70% slope) southeast to west exposures. They contained small amounts of native and non-native perennial grasses, notably bluegrasses (*Poa* spp. L.), bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. & Smith), and timothy (*Phleum pratense* L.), as well as moderate amounts of annual bromes in the steepest, rockiest portions. Although a wide variety of native and non-native forbs occurred on the sites (Appendix 1), spotted knapweed was overwhelmingly dominant. Historic photographs, grazing allotment maps, and written descriptions indicate most spotted knapweed sites were previously dominated by bluebunch wheatgrass and cheatgrass. However, eight 100 point U.S. Forest Service loop transects (Parker 1951) done in 1964 to monitor range condition give a different picture. Forbs accounted for 71% of herbaceous plant hits, perennial grasses 16%, and annual grasses 13%. Thus, while bluebunch wheatgrass and cheatgrass may have been the most abundant individual species, forbs may have been the most abundant class of herbaceous plant.

Bunchgrass/sedge vegetation type—Sites meeting the criteria for this vegetation type typically occurred on cooler microsites where plant phenology was slightly retarded compared to knapweed sites. No aspect predominated, and slopes were similar to those of knapweed sites. Bluebunch wheatgrass and Idaho fescue (*Festuca idahoensis* Elmer) were the most important grasses. The sedge component was present mainly on sites with a northerly aspect. Many sites had a significant forb component, but there was little spotted knapweed (Appendix 1).

We chose the bunchgrass/sedge vegetation type for comparison to spotted knapweed because it was the only widespread, herbaceous vegetation type dominated by native plants. It was not necessary that bunchgrass/sedge be identical to the pre-existing plant community on knapweed sites in order to test our hypothesis or to determine whether substantial numbers of cervids occurred on the knapweed vegetation type.

Almost every other day from 1 December–25 April of 1990–91 and 1991–92 we selected 1 of the 7 sites at random and surveyed cervid densities for 2 hours at a randomly selected time of day (morning, midday, or evening). Hunting season ended 10 days before surveys began, and no humans other than the researcher were present nearby during surveys. We counted cervids visible in knapweed and bunchgrass sedge at 15 min intervals (9 times in 2 hours). We then averaged the 9 counts of each cervid species for each vegetation type. We computed density by dividing average counts by area of vegetation type. Each 2 hour survey yielded 1 independent density estimate for each cervid species on each vegetation type present.

Cervid Diets

We estimated ungulate diets from analyses of rumen contents (Puglisi et al. 1978), microscopic forage fragments in feces (Sparks and Malechek 1968), and feeding sites (modified from Knowlton 1960). We used the second method for elk only. We collected rumen samples from carcasses or from viscera left by hunters October–May 1990–96. Samples were collected from a few hours to 4 months after deaths of the animals. We collected most (71%) within 1 week of the estimated date of death. Older samples were generally frozen and often had been covered with snow. These samples showed a yellowish discoloration but otherwise seemed similar to fresher samples. We believe that the activity of the animal immediately prior to death, feeding versus ruminating, probably had a more important effect on the samples than age. Animals that died while feeding, as evidenced by large food items in the mouth, generally had larger and more easily identified forage fragments in the rumen. We collected samples of elk pellets (3 pellets/group) whenever fresh pellet groups were encountered during the first 2 field seasons. At least 25 pellet groups were represented in each monthly composite sample. The Composition Analysis Laboratory at Colorado State University carried out microhistological analysis of feces. We used mean percent relative density based on 3 slides of 20 fields each to estimate elk diets from fecal samples. We studied feeding sites of elk in winter-spring 1992–93 and feeding sites of deer during the field seasons of 1992–93 and 1993–94. We observed animals feeding from 5–60 min and noted their exact path with respect to small landmarks such as sticks, rocks, bushes, etc. Then we examined this area carefully for evidence of freshly cropped vegetation. Plant species were ranked by estimates of volume consumed. Consumption of foods such as arboreal lichens or fungi was directly observed.

Nutrient Content

To estimate nutrient content of forages, we hand plucked composite samples of spotted knapweed rosette leaves, stems, and seedheads in mid-November 1991 on 7 sites used previously for a study of nutrient cycling (Merrill 1978). There, at the same time, we collected composite samples of annual grasses, perennial grasses, and forbs other than knapweed. We collected further samples of spotted knapweed rosette leaves at 3 sites near the center of the study area mid-month February, March, and April 1993. Composite samples of these forages were collected by walking diagonally upslope across plots and stopping every 10 steps to hand pluck samples from the nearest 10 plants. All samples contained portions of ≥ 100 plants.

We collected composite samples of current annual growth of redstem ceanothus (*Ceanothus sanguineus* Pursh) and new-growth bluebunch wheatgrass in January 1993 and late March 1993 respectively in areas where we observed use by deer and elk. Each sample contained portions of ≥ 100 plants.

We had all forage samples analyzed for gross energy, in vitro dry-matter digestibility (IVDMD), and crude protein by the Range Science Nutritional Analysis Laboratory at Colorado State University. Standard hay samples were tested along with forage samples during nutrient analyses for quality control.

Changes in Biomass and Available Nutrients

We compared total biomass, available digestible energy, and available crude protein on Merrill's (1978) plots from 1976 with our own measurements made in 1991. We measured total biomass again in 1992. The plots, located in the south end of the study area, had little or no spotted knapweed in 1976 but became overgrown in intervening years. Designed for other purposes, these plots did not constitute a statistical sample of the study area. However, they did appear typical of non-forested sites now dominated by spotted knapweed. We harvested biomass in mid-November on ten 20 by 50 cm subplots/plot using the same methods and at the same time of year as Merrill (1978). We oven dried and weighed harvested vegetation after sorting it into 6 categories: spotted knapweed rosettes, stems, and seedheads, other forbs, annual grasses, and perennial grasses. We made separate estimates of available digestible energy and crude protein for both 1976 and 1991 using the algorithm of Hobbs and Swift (1985). The algorithm estimates the amount of a nutrient available by sequentially adding lower quality forages to a theoretical diet until the nutrient concentration of the mix drops to the chosen constraint. The algorithm specifies that forages be sorted into categories equal to the smallest plant parts that a herbivore can select. Because Merrill's (1978) measurements were intended for another purpose, the vegetation categories were broader than the ideal. We used our November 1991 forage analyses to calculate available nutrients for 1991.

We used Merrill's data to calculate available crude protein for 1976, but because values of IVDMD were not available for 1976, categories were assumed to have the same values as in 1991. Digestible energy for each vegetative category was estimated by in vitro dry-matter digestibility (IVDMD) × gross energy

Cnicin Content

We collected composite samples of spotted knapweed stems (with leaves attached), rosette leaves, and seedheads monthly from December 1991–April 1992 and analyzed them for dry-matter content of cnicin. These composite samples were collected at 3 sites near the center of the study area as described above. Samples were oven dried at 50° C for 24 hours and sealed in plastic bags for storage. One of the stem samples was divided in half. One half was processed without separating the tissues, while the other half was sorted into stems and stem leaves and thereafter treated as separate samples. Samples were extracted and analyzed by HPLC using conditions similar to Olson and Kelsey (1997).

Statistical Analyses

For each cervid species and their combined total we tested equality of densities between knapweed and bunchgrass/sedge using a blocked, strip-plot design with analysis of variance (ANOVA). Analysis was restricted to the 4 sites where both vegetation types occurred. Variation between sites and years was removed from the error term by considering each site in each year as a separate block. Vegetation type and season were the main effects of the strip-plot. All data sets required transformation (natural log + 0.01) to insure homogeneous variances and normality.

We compared rumen contents among 3 cervid species with multivariate analysis of variance (MANOVA). The model specified food types (arcsine square root transformed % rumen contents) as dependent variables and cervid species as the main effect. We assessed seasonal changes in knapweed use at feeding sites with G^2-tests of independence. Frequencies of food type ranked 1 in use (knapweed or other) were listed by 3 seasonal periods in a 2 × 3 contingency table. Equality of fall biomass on sample plots before and after knapweed infestation was tested with a t-test.

For nutrient and cnicin content analyses we formed composite tissue samples from many plants on a variety of sites versus many replicates from individual plants. This approach (Cook and Stubbendick 1986) made it possible to estimate central tendency for characteristics across the range of sites available. The alternative approach would provide a precise estimate for several plants while limiting inferences concerning sites across the study area.

Results

Cervid Densities

Sizeable densities of all 3 cervid species were observed on the spotted knapweed vegetation type (Table 1). Where both spotted knapweed and bunchgrass/sedge occurred on the same site, a significant vegetation type effect existed in the ANOVA model for elk (P = 0.048) and all cervids combined (P = 0.031). A near significant effect existed for white-tailed deer (P = .081) (Table 2). Although density estimates were highest 1 March–25 April for all cervid species on both vegetation types, there were no significant season or season × vegetation type effects in any model. White-tailed deer were never observed in the bunchgrass/sedge type during a survey and were seldom seen there at other times.

Table 1. Estimated densities (number/ha) of cervids on unforested spotted knapweed vegetation type in the Selway River drainage. Idaho during winter-spring 1990–91 and 1991–92.

	Time Period[1]					
	1 Dec.–15 Jan.		16 Jan.–28 Feb		1 Mar.–25 Apr.	
	$\overline{X}$	SE	$\overline{X}$	SE	$\overline{X}$	SE
	(no./ha)					
Elk	0.22	0.06	0.19	0.07	0.30	0.06
Mule deer	0.03	0.01	0.08	0.03	0.17	0.05
White-tailed deer	0.01	0.01	0.03	0.01	0.05	0.02

[1]n = 39, 37, and 44 for 1 Dec.–15 Jan., 16 Jan.–28 Feb., and 1 Mar.–25 Apr. respectively.

Table 2. Geometric means and standard errors (+, -) for estimated cervid densities (number/ha) on unforested vegetation types in the Selway River Drainage, Idaho during 66 scan surveys in winter-spring 1990–91 and 1991–92.

Cervid Species	Vegetation Type: Spotted knapweed	Vegetation Type: Bunchgrass/ sedge	P[1]
	(no./ha)		
Elk	0.040 (+ 0.013, - 0.010)	0.014 (+ 0.006, - 0.005)	0.048
Mule deer	0.011 (+ 0.004, - 0.003)	0.007 (+ 0.003, - 0.002)	0.338
White-tailed deer	0.006 (+ 0.003, - 0.002)	0.000 (invariant)	0.081
All species	0.073 (+ 0.022, - 0.017)	0.024 (0.009, - 0.007)	0.031

[1]P-value is for vegetation type effect in ANOVA.

Cervid Diets

Rumen contents varied among cervid species (P < 0.001) (Table 3). Cervid species was a significant or near-significant effect for every forage category in the analysis except conifers, knapweed stems, and miscellaneous items. We interpret the first canonical axis, which accounts for 92% of the data set variability, as separating elk, represented by large shrub and grass weightings, from deer, represented by high within structure negative correlations for knapweed rosette leaves and other forbs (Table 4). The second axis tends to separate the 2 deer species, but sample sizes are too small to make further interpretation useful. We collected deer rumens containing > 20% rosette leaves in October, November, March, and May (Table 5). Microhistological analysis of elk fecal samples yielded monthly estimates from 2–20% spotted knapweed with consumption highest during April both in 1991 and 1992 (Fig. 1).

Type of food ranked 1 (spotted knapweed versus any other) at feeding sites was not independent of season for elk (P = 0.048, n = 70), mule deer (P = 0.002, n = 67), or white-tailed deer (P < 0.001 n = 73). For all 3 cervid species we observed heaviest use of spotted knapweed seedheads 1 December–15 January and heaviest use of rosette leaves 1 March–25 April (Tables 6, 7, and 8).

Table 3. Contents (% volume) of the rumens of cervids found dead near the Selway River, Ida. Oct.–May 1990–96.

	Elk n = 34		Mule Deer n = 8		White-tailed Deer n = 14		
Forage	$\overline{X}$	SE	$\overline{X}$	SE	$\overline{X}$	SE	P[1]
	(% vol.)						
Shrubs	38	6	15	6	18	8	0.059
Conifers	5	1	29	15	9	6	0.106
Grass-like	47	7	7	5	1	1	< 0.001
Forbs							
Centaurea maculosa							
rosette	1	0	34	15	24	10	< 0.001
seedhead	3	1	2	2	trace		0.034
stem	1	0	trace		trace		0.448
Other Forb	5	3	10	8	44	11	< 0.001
Other	1	0	2	1	3	1	0.106

[1]P- value for greater F in MANOVA for species effect on forage 2, 45 df.

Table 4. Standardized canonical coefficients and within canonical structure for first axis of MANOVA model with forage content of cervid rumens predicted by cervid species. Rumens collected Oct.–May 1990–96 in Selway River drainage, Idaho.

Forage	Standardized Canonical Coefficients	Within Canonical Structure
Shrubs	1.5585	0.2076
Conifers	0.2661	-0.0941
Grass-like	2.0575	0.4800
Forbs		
Centaurea maculosa		
rosette	0.2413	-0.3606
seedhead	0.3802	0.2201
stem	0.2256	0.1087
Other Forb	0.3745	-0.3365
Other	0.0336	-0.1743

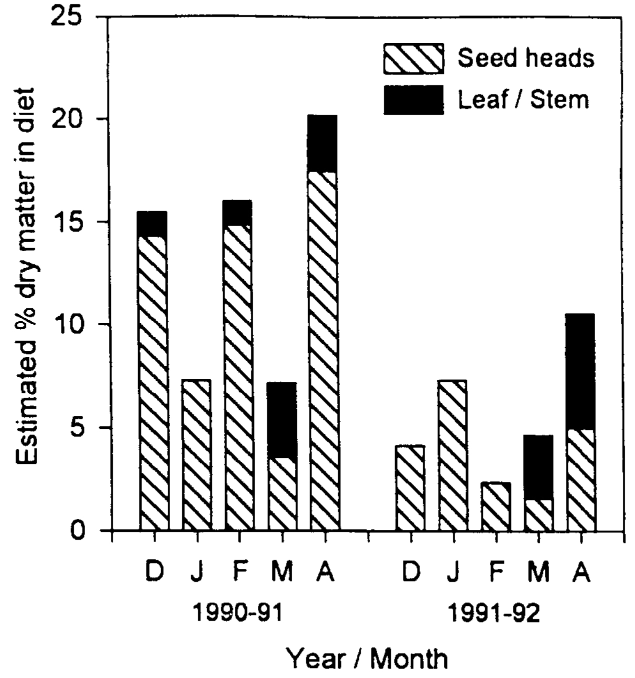

Fig. 1. Percentage of spotted knapweed in elk diets in the Selway River drainage, Idaho during 2 winter-spring periods as estimated by microhistological analysis of fecal pellets.

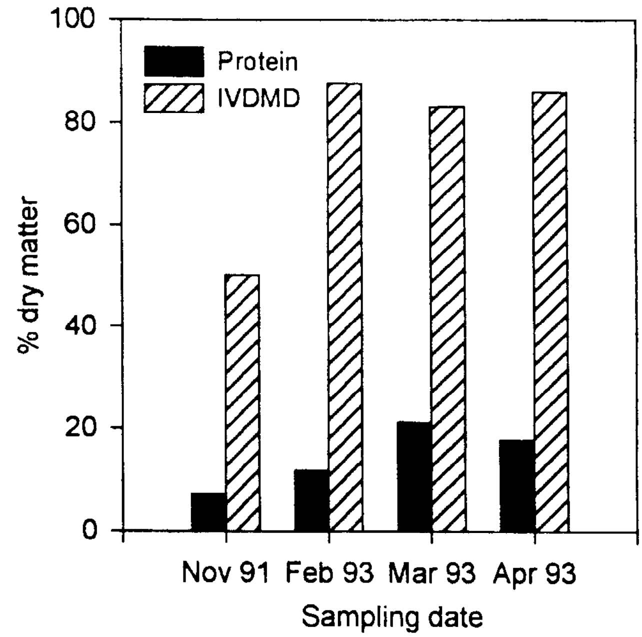

Fig. 2. Crude protein and in vitro dry-matter digestibility of composite samples of spotted knapweed basal rosette leaves collected near the Selway River, Ida.

Nutrient Content

The nutritional value of spotted knapweed rosette leaves was much higher in spring than fall (Fig. 2). Highest values of IVDMD, 88%, were measured in mid-February at the time seasonal growth was just beginning. Crude protein peaked in mid-March at 21.2% dry matter.

The nutritional value of rosette leaves was greater than that of other plant parts in November 1991. Crude protein was measured as 4.7% for seedheads and 2.7% for stems with leaves versus 7.1% for rosette leaves. November IVDMD was 45% for seedheads, 40% for stems with leaves, and 50% for rosette leaves. During mid-January 1993 when utilization of current annual growth of redstem ceanothus was so heavy that a sample was difficult to collect, crude protein was measured as 7.9%, gross energy as 4,388 cal/g and IVDMD as 48%. For new-growth bluebunch wheatgrass during peak utilization in late March, values of these same parameters were 25.1%, 4326 cal/g, and 85%.

Table 5. Content (% volume) of spotted knapweed found in deer rumens from the Selway River, Ida. Oct.-May 1990–96.

Species	Date	Plant tissue Seedheads	Rosettes	Stems
		---------- (% vol.)----------		
White-tailed	22 October	0	91	0
White-tailed	22 October	0	97	trace
Mule	31 October	trace	99	trace
White-tailed	1 November	0	8	0
White-tailed	4 November	0	18	1
White-tailed	5 November	trace	trace	trace
White-tailed	6 November	0	20	0
Mule	11 November	trace	83	1
White-tailed	15 November	0	92	1
White-tailed	16 November	0	8	0
White-tailed	17 November	1	trace	0
White-tailed	12 December	0	0	0
White-tailed	15 December	trace	0	0
Mule	28 December	0	0	0
White-tailed	7 January	0	0	0
White-tailed	14 January	0	0	0
Mule	19 January	0	0	0
White-tailed	6 February	0	trace	0
Mule	20 February	0	0	0
Mule	20 February	14	0	0
Mule	26 March	0	21	0
Mule	7 May	trace	69	0

Changes in Biomass and Available Nutrients

The standing crop of fall biomass on 7 rangeland plots increased after knapweed infestation ($P \leq 0.05$) (Fig. 3). While biomass of knapweed increased from 0 to near 40 g/m^2, biomass of annual grasses stayed nearly constant. However, there was a dramatic decrease in biomass of perennial grasses and forbs other than knapweed. The fall standing crop of digestible energy (kcal/m^2) and crude protein (g/m^2) was higher post-invasion (Figs. 4 and 5 data points farthest to the left). However, because much of the increase was composed of low-digestibility spotted knapweed stems, more digestible energy would have been available pre-invasion if animals consumed only diets exceeding 2 kcal/g digestible energy (Fig. 4). Assuming ≤ 10% of the forage consumed by cervids would consist of knapweed stems, available digestible energy was lower post-invasion. Crude protein available post-invasion remained near or above pre-invasion levels regardless of minimum dietary constraints (Fig. 5). With knapweed stems ≤ 10% of the diet, available crude protein was lower post-invasion at minimum dietary constraints ≤ 5.5% crude protein.

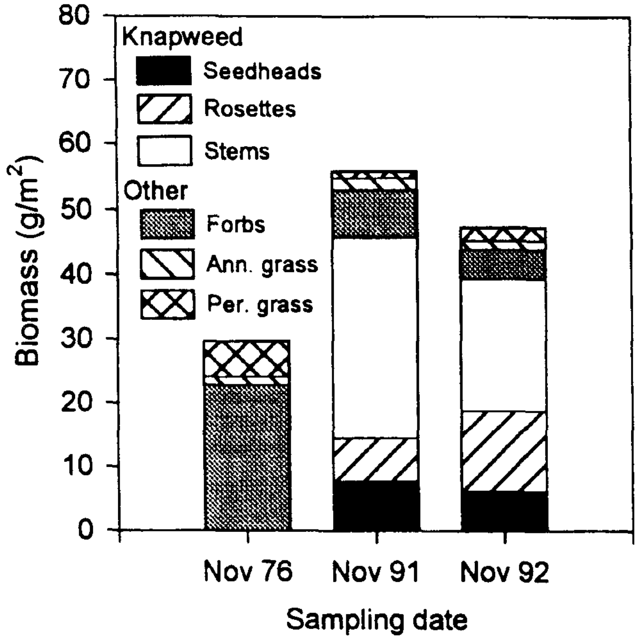

Fig. 3. Mean biomass on 7 rangeland plots near the Selway River, Ida. before (1976) and after (1991, 1992) spotted knapweed invasion. Data for 1976 is from Merrill (1978).

Cnicnin Content

Spotted knapweed seedheads contained the lowest cnicin concentrations of any plant part while rosette leaves consistently showed much higher concentrations (Fig. 6). Stems and stem leaves combined contained intermediate concentrations. Leaves removed from stems contained the highest concentrations of any tissue as previously reported (Locken and Kelsey 1987). Cnicin concentrations remained relatively constant in senescent tissues from December–April and did not increase in rosette leaves with the onset of spring growth.

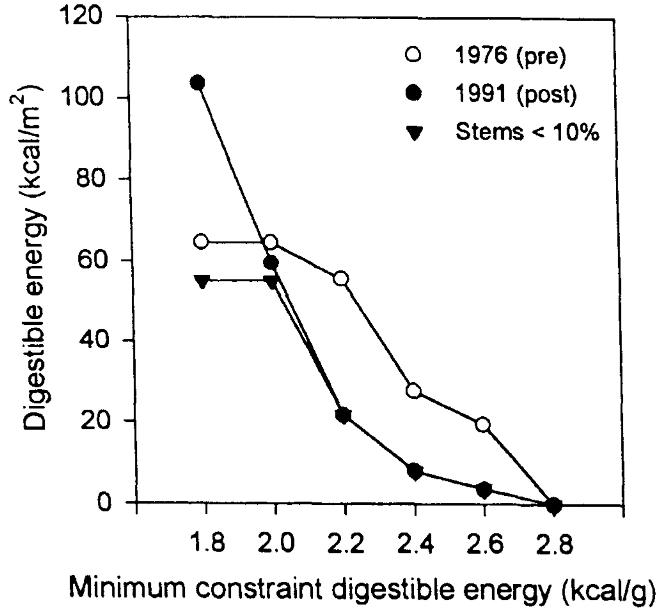

Fig. 4. Available digestible energy at various minimum dietary constraints on 7 rangeland plots near the Selway River, Idaho. Spotted knapweed was present only in trace amounts in 1976, but plots were heavily infested prior to 1991. Biomass data for 1976 taken from Merrill (1978).

Discussion

We found no evidence that spotted knapweed infestation caused a dramatic reduction in the carrying capacity of the Selway winter-spring range. Consistent with this observation, aerial counts and harvest data for elk and deer do not show a downward trend from 1971–1991 (Kuck and Nelson 1991). However, other factors in the ecosystem such as changes in hunting harvest, post-burn plant succession, amelioration of winter climate, and 6 decades of fire suppression may obscure the effects of infestation on populations.

Elk and deer used the knapweed vegetation type as much or more than the bunchgrass/sedge during 1 December–25 April. Knapweed seedheads were one of the few herbaceous plants readily available to elk and deer in open areas when snow depths

Table 6. Common food plants of elk in the Selway River drainage, Idaho as determined by feeding site examination during winter-spring of 1992–93. Percent frequency is the proportion of feeding sites where the food item was eaten regardless of amount. Zero values omitted for readability.

Food item	1 Dec. –15 Jan. (n = 26) Times ranked 1		16 Jan.–28 Feb. (n = 22) Times ranked 1		1 Mar.–25 Apr. (n = 22) Times ranked 1	
	(%)	(% freq)	(%)	(% freq)	(%)	(% freq)
Shrubs						
Acer glabrum	3	(15)		(4)		
Amelanchier alnifolia	35	(65)	23	(45)		(9)
Ceanothus sanguineus	23	(42)		(4)		(5)
Rhamnus purshiana	8	(19)				
Salix spp.	4	(4)		(4)		
Conifers						
Psuedotsuga menziesii		(15)	5	(9)		
Thuja plicata	3	(4)				
Grass-like						
Agropyron spicatum		(8)	9	(14)	14	(50)
Bromus (annual)					4	(9)
Carex spp.	4	(19)	14	(32)	18	(64)
Festuca idahoenis			4	(9)	5	(14)
Poa spp.		(4)		(9)	5	(9)
unknown grass		(4)		(18)	5	(50)
Forbs						
Centaurea maculosa						
rosette	8	(19)	45	(55)	50	(91)
seedhead	8	(38)		(23)		
stem	4	(15)		(9)		

Table 7. **Common food plants of mule deer in the Selway River drainage, Idaho as determined by feeding site examination during winter-spring of 1992–93 and 1993–94. Percent frequency is the proportion of feeding sites where the food item was eaten regardless of amount. Zero values omitted for readability.**

Food item	1 Dec. –15 Jan. (n = 17) Times ranked 1		16 Jan.–28 Feb. (n = 21) Times ranked 1		1 Mar.–25 Apr. (n = 29) Times ranked 1	
	(%)	(% freq)	(%)	(% freq)	(%)	(% freq)
Shrubs						
Amelanchier alnifolia	41	(82)	24	(52)		(7)
Ceanothus sanguineus	6	(18)	5	(19)	4	(3)
Ceanothus velutinus	12	(18)				
Conifers						
Pseudotsuga menziesii		(12)	5	(19)		
Grass-like						
Agropyron spicatum	6	(24)		(43)	4	(21)
Bromus (annual)			5	(10)		(21)
Poa spp.					3	(7)
unknown grasses				(24)	14	(28)
Forbs						
Achillea millefollium		(6)		(10)	3	(14)
Centaurea maculosa						
seedhead	18	(41)	10	(38)		(7)
rosette		(12)	29	(48)	69	(93)
stem						(3)
Hieracium spp.			4	(10)	3	(3)
Phacelia spp.			4	(19)		(10)
Dianthus armeria	5	(6)	4	(10)		(17)
Other						
Arboreal lichens	12	(24)	10	(30)		

exceeded 30 cm. Cow and calf elk rarely pawed feeding craters, presumably because palatable browse was readily available. Knapweed rosette leaves were available to cervids on open south slopes as soon as snowmelt began and feeding animals were commonly observed on these sites through spring. Our findings differ from those reported by Willard et al. (1988) for the Bitterroot Valley. They reported minimal use of knapweed-dominated open areas by elk and deer, which, when feeding on spotted knapweed used primarily seedheads. However, on their study areas, deer and elk densities were low, agricultural habitats were available nearby, and there was less snow cover.

Unlike mule deer, white-tailed deer made little use of bunchgrass/sedge and conditions for this species probably improved when cheatgrass and drier bunchgrass sites were invaded by knapweed. We suspect the competitive relationship between the 2

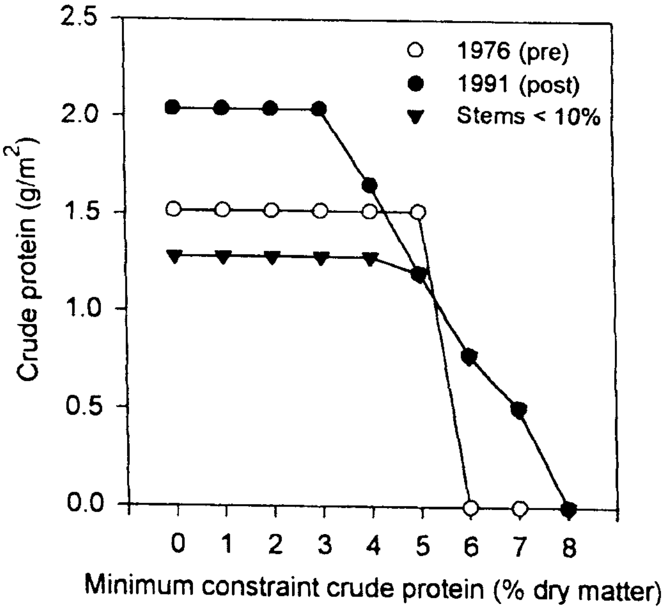

Fig. 5. Available crude protein at various minimum dietary constraints on 7 rangeland plots near the Selway River, Idaho. Spotted knapweed was present only in trace amounts in 1976, but plots were heavily infested prior to 1991. Data for 1976 is from Merrill (1978).

deer species may have altered to the benefit of the white-tailed deer as a result of knapweed infestation.

All 3 methods used to assess cervid diets have previously been recognized as biased under some circumstances (Gill et al. 1983,

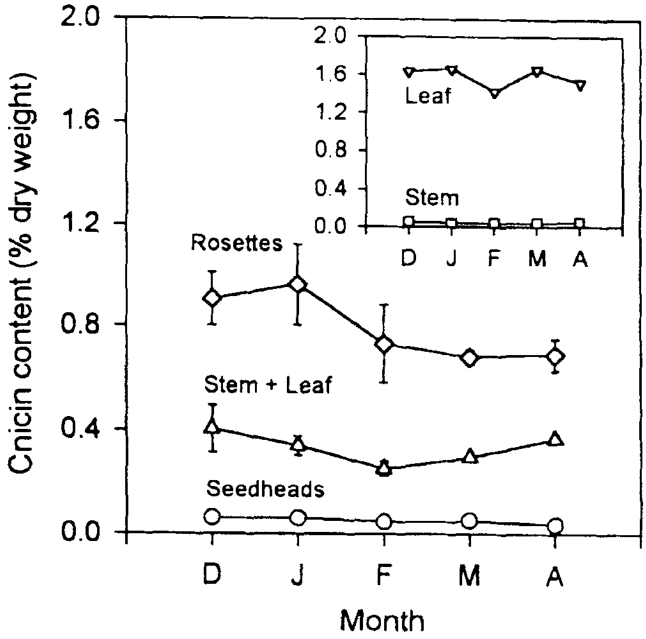

Fig. 6. Mean cnicin content ± SE from composite samples of spotted knapweed gathered near the Selway River, Idaho in 1993. Insert shows differences in cnicin concentrations between stems and leaves attached to stems at 1 of the collection sites.

Table 8. Common food plants of white-tailed deer in the Selway River drainage, Idaho as determined by feeding site examination during winter-spring of 1992-93 and 1993-94. Percent frequency is the proportion of feeding sites where the food item was eaten regardless of amount. Zero values omitted for readability.

Food item	1 Dec. –15 Jan. (n = 19) Times ranked 1		16 Jan.–28 Feb. (n = 24) Times ranked 1		1 Mar.–25 Apr. (n = 30) Times ranked 1	
	(%)	(% freq)	(%)	(% freq)	(%)	(% freq)
Shrubs						
Amelanchier alnifolia	11	(32)	13	(42)		(10)
Arctostaphylos uva-ursi		(5)	4	(8)		
Berberis repens	5	(21)	8	(25)		(10)
Ceanothus sanguineus	16	(32)		(8)		
Salix spp.		(5)	8	(13)		(3)
Conifers						
Abies grandis	5	(16)				
Grass-like						
Festuca idahoenis					3	(6)
Phleum pratense	5	(11)		(33)		(37)
Unknown grasses		(5)		(13)	3	(37)
Forbs						
Centaurea maculosa						
seedhead	16	(42)		(21)		
rosette	26	(53)	42	(86)	90	(94)
stem	5	(16)		(13)		(3)
Coptis occidentalis			4	(4)		
Dianthus armeria		(11)	8	(21)		(33)
Other						
Arboreal Lichens	5	(16)	13	(17)	4	(3)
Mushrooms	6	(6)				

Holechek et al. 1982, Kessler et al. 1981). Rumen analyses may have underestimated the proportion of spotted knapweed rosette leaves in diets because: 1) foliar material readily separated from leaf mid-veins and broke into small fragments, and 2) cervid mortality occurred disproportionately in forest habitats and during periods of deep snow cover. Feeding site data may have exaggerated knapweed use because animals were more visible in open habitats where the plant was prevalent. Feeding site data did demonstrate that cervids ate knapweed when in those habitats. We did not attempt to establish correction factors for fecal analysis because forage classes each contained a diversity of species (Gill et al. 1983). While our methods were unable to give a reliable quantitative estimate of knapweed content in the diet, all methods indicated spotted knapweed was a significant food plant for elk. In contrast, both feeding site data and the small number of deer rumens collected suggest spotted knapweed may have been a major food plant for mule deer and white-tailed deer during October–November and March–May. As concentrate feeders (Hobbs et al. 1983), deer may be better morphologically and physiologically adapted to eating rosette leaves than elk.

The nutritional value of rosette leaves compared well with that of redstem ceanothus in winter and new-growth bluebunch wheatgrass in spring. However, leaves are small in winter and often under snow. Seedheads, though of lower nutritional value, require little search effort and become an attractive food source when snow and heavy utilization make better forages less available. Increased use of rosette leaves in spring probably was due to snowmelt and improved nutritional value rather than increased biomass, since growth was slow prior to mid-April.

Conventional wisdom has held that knapweed infestations bring about severe (80 to 90%) reductions of forage production on wildlife ranges (Harris and Cranston 1979; Reel 1989). However, fall biomass was higher on our study plots after infestation. This could not be attributed to rainfall differences among years as rainfall in the preceding 12 months measured 76 cm, 48 cm, and 61 cm in 1976 (pre-invasion), 1991 (post-invasion) and 1992 (post-invasion), respectively. Tisdale (1976) documented another case where rangeland yielded more biomass when dominated by a near-monoculture of an invasive weed than when occupied by a more diverse plant community. He found total herbage yields were reduced after biological control of goatweed although yields of annual forbs and grasses increased. The forage production referred to in other studies may not include knapweed (see Table 1 in Watson and Renney 1974, Hubbard 1975). In other cases forage production on infested plots was compared to plots where infestation was controlled by treatments such as burning, seeding, or fertilizing (Roche 1991) that may temporarily stimulate productivity.

Although an estimate of nutrient availability using the algorithm of Hobbs and Swift (1985) is an artificial construct with obvious shortcomings, it is nonetheless a refinement over merely measuring standing crop of a nutrient. If the entire spotted knapweed plant is considered available for consumption, as much or more energy and protein was available at acceptable concentrations in forage after invasion by knapweed. Possibly, the low digestibility of knapweed stems plus the metabolic costs associated with secondary compounds in stem leaves could limit the proportion of stems in cervid diets even at high population densities. If cervids limited the proportion of spotted knapweed stems in their diets to ≤ 10%, our data suggests a modest reduction in carrying capacity of infested areas may have occurred.

Because some sesquiterpene lactones are herbivore feeding deterrents (Picman 1986), the value of spotted knapweed as a cervid food cannot be fully understood without considering the effects of cnicin. Studies in western Montana have found this sesquiterpene lactone, located in glandular trichomes on the surfaces of stems and leaves (Locken and Kelsey 1987), present in some tissues at ≥ 1% dry weight (Kelsey and Mihalovich 1987). Antibacterial properties (Cavalito and Bailey 1949, Vanhaelen-Fastre 1972) could affect rumen flora (Olson and Kelsey 1997) and limit knapweed use by elk and deer. Cnicin concentrations in the rosette leaves decreased somewhat in March-April relative to December–January. The low tissue concentration coincided with an increase in utilization by all 3 cervid species. However, because the spring decrease was small, increased utilization was probably caused by other factors such as increased tissue nutrient content and increased availability with snowmelt and the onset of growth. Because some rumen samples contained large volumes of spotted knapweed (maximum of 15% for elk, 99% for mule deer, and 97% for white-tailed deer), and because cervids utilized knapweed well into the spring when other forages were abundant, cnicin does not appear to be an effective feeding deterrent. It does, however, fit the profile of a generalist insect feeding deterrent (Stipanovic 1983) and might provide a chemical defense against some insect or mammalian herbivores later in the growing season when flower heads and seeds are developing. Other secondary compounds are present in spotted knapweed at lesser concentrations (Kelsey and Bedunah 1989). Their effects on ingestion and digestion of spotted knapweed by cervids are unknown.

There may be situations where expensive campaigns to control well established spotted knapweed on cervid winter-spring ranges are justified. For example, at urban-agricultural/wilderness interfaces where a small remnant of such habitat is managed to divert elk and deer from damaging private property, intensive measures such as chemical treatment or even supplemental feeding may be needed. In the Selway, an intact, wilderness range, cervids cannot move short distances to reach fertilized lawns or fields. Here, they use the knapweed vegetation type, they feed on the plant, and they obtain significant nutrition doing so. The diets cervids will consume on any given winter-spring range depends on many local factors, and we make no attempt to predict this. Clearly, given high enough animal densities and limited choices, elk and deer will consume spotted knapweed. When estimating or predicting carrying capacity of a cervid range this species needs to be considered a potential food. Predictions of large declines in carrying capacity accompanying infestation should not be made without a firm rationale.

We believe resources allocated to control of spotted knapweed in central Idaho should be directed to preventing invasion of new areas and establishing biological control agents. Managers should recognize that reducing knapweed density without filling the empty niches with desirable species may encourage the proliferation of other exotics that are more unpalatable, toxic, spiny, or otherwise noxious than knapweed (Muller-Scharer and Schroeder 1993). Sulfur cinquefoil (*Potentilla recta* L.) which is already widespread and increasing in the Selway has a high tannin content and appears to be less palatable to ruminants than spotted knapweed (Rice et al. 1991). The Selway and similar areas should not be written off as sacrifice zones to noxious weeds. Education of wilderness users and management agency employees, and regular removal of new exotic plant species at trailheads, campsites, and along road corridors need to begin immediately.

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Appendix 1. Forb species found on unforested sites dominated by spotted knapweed and bunchgrass/sedge in the Selway-Bitterroot Wilderness. Cervid densities were measured on these sites during winter-spring of 1990-91 and 1991-92. "Common" species were those estimated to exceed 1% of vegetation coverage in early fall on some sites. Invasive exotics indicated with a *.

Forb Species	Vegetation Type	
	Knapweed	Bunchgrass/sedge
Achillea millefolium	common	common
Antennaria racemosa		
Apocynum androsaemifolium		
Arenaria congesta		
Arenaria nuttallii	common	
Aster spp.		
Balsamorhiza sagittata		common
Brodiaea spp.		
Campanula rotundifolia		
Castilleja spp.	common	common
*Centaurea maculosa**	common	
Cerastium arvense	common	
*Chrysanthemum leucanthemum**		absent
Clarkia pulchella	common	common
Claytonia lanceolata		
Clematis columbiana	absent	
Collinsia parviflora		
Collomia grandiflora		
Collomia linearis		
Cuscuta spp.		absent
Delphinium spp.		common
*Dianthus armeria**	common	
Dodecatheon pulchellum	absent	
Draba spp		
Draba verna		
Epilobium spp.	common	common
Eriogonum spp.		
Erysimum spp.	absent	
*Erigeron strigosus**		
Erythronium grandiflorum	absent	
Fritillaria pudica	absent	
Geranium bicknellii		
Gilia spp.		
Hieracium spp.		common
Helianthella uniflora		
Heuchera spp.	absent	
Hydrophyllum capitatum		
Hydrophyllum fendleri	absent	
*Hypericum perforatum**		common
Lactuca spp.	absent	
Lithophragma parviflora	common	
Lomatium spp.		common
Lonicera ciliosa	absent	
Lupinus		
Madia spp.		absent
Mertensia spp.		
Microsteris gracilis		
Mimulus spp.	absent	
Montia perfoliata		
Myosotis spp.		
Oenothera spp.		
Phacelia heterophylla		common
Phacelia linearis		
Penstemon spp.		
Polygonum spp.		
Potentilla glandulosa		common
*Potentilla recta**		absent
*Ranunculus acris**	absent	
Ranunculus spp.		
Rumex acetosella		
Sedum spp.		
Senecio integerrimus		
Sisyrinchium spp.	absent	
Spiranthes romanzoffiana	absent	
Thermopsis montana	absent	
Thlaspi fendleri		
Tragapogon dubius		common
*Trifolium agrarium**		
Trifolium latifolium		
Triodanis perfoliata		
Viola spp.	absent	
Zigadenus venosus		