

## Winter Foraging Response of Elk to Spotted Knapweed Removal

### Abstract

Picloram was used to convert 110 ha of an historically cultivated grassland (hereafter old-field) from spotted knapweed (*Centaurea maculosa*) to grass on an elk (*Cervus elaphus*) winter range in western Montana. About 30 ha were left untreated. I hypothesized that knapweed removal would not: (H<sub>0</sub>I) affect winter foraging activity of elk; (H<sub>0</sub>II) affect winter diets; (H<sub>0</sub>III) vary in its effects on foraging activity and diets across the first four winters after knapweed removal; and (H<sub>0</sub>IV) affect elk population distribution. Elk walked in adjacent knapweed and grass stands indiscriminately, but foraged almost exclusively in the grass stand (H<sub>1</sub>I). Diets sampled before and after knapweed removal were not rank correlated, and forages characteristic of the old-field (i.e., *Poa*, *Bromus*, *Phleum*) ranked higher in diets after knapweed removal (H<sub>1</sub>II). Elk foraging activity was significantly higher in the first winter than in subsequent winters (H<sub>1</sub>III). A higher proportion of the estimated elk population used the old-field after knapweed removal (H<sub>1</sub>IV). I concluded that abundant green grass attracted elk to the old-field in the first winter after knapweed removal. Cured grass apparently attracted elk foraging activity and affected winter diets to a lesser extent in subsequent winters. When planning knapweed removal, elk managers should consider preexisting range condition and knapweed density, occurrence of preferred forage species, current and desired elk distribution, and the probability of adequate rainfall for substantial grass growth in the first growing season after herbicide application.

### Introduction

Knapweeds (*Centaurea* spp.) are Eurasian species occurring on over five million hectares in the northwest United States and southwest Canada (Lacey 1989). Annual production of spotted knapweed (*C. maculosa*) may exceed 1,000 kg/ha on disturbed rangelands near roadside seed sources (Carpenter 1986). Tyser and Key (1988) also reported the invasion of spotted knapweed (hereafter knapweed) into relatively pristine fescue grasslands with a coincident decline in native plant diversity.

Winter ranges of Rocky Mountain elk (*Cervus elaphus nelsoni*) typically include rangelands (Lyon and Ward 1982) vulnerable to knapweed invasion (Mooers 1986). Elk are not obligate grazers, as evidenced by the 151 winter forages listed by Nelson and Legee (1982), but may lose foraging efficiency (Wickstrom et al. 1984) where knapweed dominates productive grasslands. Although speculative, an unpublished Forest Service report (Spoon et al. 1983) has often been referenced to justify warnings of future elk declines as knapweed spreads (Lolo National Forest 1991). Bedunah and Carpenter (1989) extrapolated the results of herbicide trials to imply a potential 2.4-fold increase in range carrying capacity for elk following knapweed control and concurrent grass production gains. However, results reported by

Lavelle (1986) suggest elk can incorporate knapweed into their winter diets. Participants at the 1989 Knapweed Symposium identified knapweed impacts on elk winter ranges as a research need (Fay and Lacey 1989).

In May 1989, knapweed was removed from most of an historically cultivated grassland (hereafter old-field) on an elk winter range in western Montana. This vegetation conversion provided an unusual opportunity to study elk dietary responses because the vegetation composition of the old-field was unique in comparison with surrounding habitats; thus, dietary changes caused by old-field treatments presumably would be indicated by corresponding changes in proportions of old-field grasses in elk feces. I hypothesized that knapweed removal would not: (H<sub>0</sub>I) affect winter foraging activity of elk; (H<sub>0</sub>II) affect winter diets; (H<sub>0</sub>III) vary in its effects on foraging activity and diets across the first four winters after knapweed removal; and (H<sub>0</sub>IV) affect elk population distribution.

### Study Area

The study focused on a 140-ha old-field in the northwest portion of the Threemile Wildlife Management Area (TWMA), located in Ravalli County, Montana (Figure 1). The old-field is 1,340-1,460 m above sea level on the west slope of the Sapphire Mountains and normally receives 32 cm of

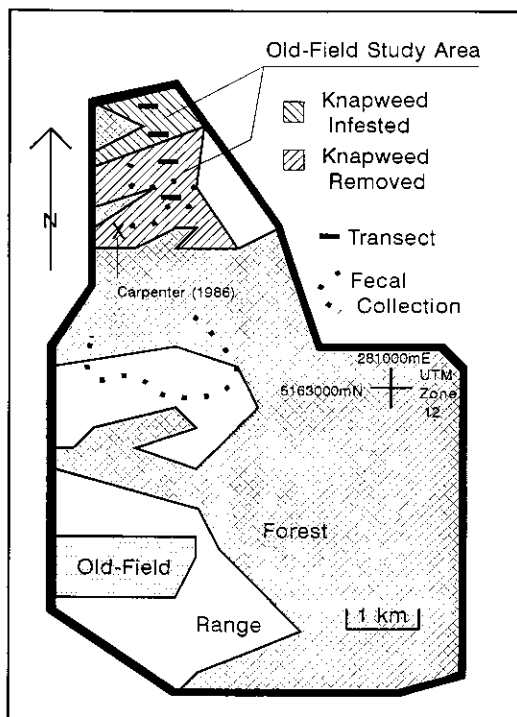


Figure 1. Juxtaposition of study sites and vegetation zones within the winter home range (adapted from Beall [1974:70], heavy outline on figure) of the Threemile elk population, 1990-1993.

annual precipitation (Carpenter 1986). It is part of an ecotone between ponderosa pine (*Pinus ponderosa*) forest and native rangeland dominated by bluebunch wheatgrass (*Agropyron spicatum*), Idaho fescue (*Festuca idahoensis*), needlegrass (*Stipa* spp.) and arrowleaf balsamroot (*Balsamorhiza sagittata*). Livestock had been excluded since 1967, when the Montana Department of Fish, Wildlife and Parks (MDFWP) purchased the TWMA to maintain and enhance elk winter range.

Knapweed dominated the old-field by 1973 (Hakim 1975). Carpenter (1986) and Bedunah and Carpenter (1989) conducted herbicide trials on 2 ha of the old-field in 1985-1988 (Figure 1). On their control plots, annual production averaged 1,234.6 kg/ha knapweed and 711.7 kg/ha grasses, compared with 8.0 kg/ha knapweed and 1,582.9 kg/ha grasses on picloram-treated plots (Carpenter 1986). Prairie junegrass (*Koeleria macrantha*) and Kentucky bluegrass (*Poa pratensis*) increased significantly after treatment. Other grasses in the old-field included cheatgrass (*Bromus tectorum*),

western wheatgrass (*A. smithii*), timothy (*Phleum pratense*), Idaho fescue, bulbous bluegrass (*Poa bulbosa*), and Canada bluegrass (*P. compressa*). Forbs and woody species were uncommon in the old-field.

On 5 May 1989, picloram was aerially broadcast (200 cc/ha) over about 110 ha of the old-field. About 30 ha were left untreated (Figure 1). D. J. Bedunah (pers. comm.) agreed the vegetation response to picloram visually resembled that measured during the earlier herbicide trials by Carpenter (1986) and Bedunah and Carpenter (1989). An abrupt demarcation between the grass (picloram-treated) and knapweed (untreated) stands was conspicuous from September 1989 through 1993. Grass growth in the old-field after knapweed removal began late in the 1989 growing season, and was likely stimulated by above-normal July-August rainfall. Grasses remained green through the first winter, but grass phenology returned to normal in subsequent growing seasons. Temperatures and precipitation were broadly similar across the four winters of study. The old-field generally was snow-covered in December-February and snow-free in March.

## Methods

Unless otherwise stated, 1990 denotes December 1989-February 1990 (the first winter of study); likewise, 1993 denotes December 1992-February 1993 (the fourth and final winter of study).

### H<sub>0</sub>I: Foraging Activity

I counted track-trails (not individual tracks) and feeding craters in the snow as evidence of elk foraging activity in the old-field knapweed and grass stands during 1990-1993. Four parallel belt transects (2 x 80 m) were established for counting tracks and craters on each side of the demarcation between the knapweed and grass stands (Figure 1). Transects were either 50 or 400 m (approximately) from the demarcation. Sampling frequency depended upon enough snow to cover grass foliage and previously counted track-trails (hereafter tracks). Mean track and crater counts in the knapweed and grass stands were tested for differences using a paired t-test.

### H<sub>0</sub>II: Diets

Composite winter diets of elk were estimated by fecal analysis (Stewart 1967, Table 1). Fecal pellets

TABLE 1. Fecal-sampling design for estimating five winter diets of elk on the Threemile Wildlife Management Area. Each diet represented a corresponding composited sample of 1-2 pellets from each of N individual pellet-groups.

Diet	Elk Pellet-Groups		
	N	Location	Representation
GRAS90	250	Old-field	First winter after knapweed removal (pellets collected on 25 February 1990); diet potentially affected by knapweed removal
GRAS91	80	Old-field	Second winter after knapweed removal (pellets collected on 3 February 1991); diet potentially affected by knapweed removal
GRAS93	250	Old-field	Fourth winter after knapweed removal (pellets collected on 22 March 1993); diet potentially affected by knapweed removal
KNAP90	82	1-3 km south of old-field	First winter after knapweed removal (pellets collected on 25 February 1990); diet potentially unaffected by knapweed removal
KNAP86	38	Old-field and immediate vicinity	Four winters before knapweed removal (data from Lavelle [1986], pellets collected December 1985-March 1986)

deposited during the current winter period were identified by color and shape (Eberhardt and Van Etten 1956). I was unlikely to mistakenly collect summer and fall depositions because most elk migrated to the study area in late November. Early-spring biases were avoided by selecting against freshly deposited pellets during late-winter collections. Composite samples included 1-2 pellets from many pellet-groups to incorporate a representative range of animal and temporal variation (Table 1). Microhistological analyses were performed by the Wildlife Habitat Laboratory at Washington State University, Pullman.

Diets of elk in the old-field were compared among four winters (Table 1); i.e., one (GRAS90), two (GRAS91) and four (GRAS93) winters after picloram treatment, and four winters before treatment (KNAP86). I sampled a fifth diet (KNAP90) to test for temporal-enhanced variation between the KNAP86 and GRAS90 diets. My sampling objective for the KNAP90 diet was to represent the same combination of foraging habitats which yielded the KNAP86 diet. Accordingly, I sampled the KNAP90 and all other diets within the winter home range of the Threemile elk population (as delineated by Beall [1974]). By subjective assessment of track patterns, I concluded that the influence of the picloram-treated old-field could be excluded from the KNAP90 sample by collecting pellets 1-3 km south of the old-field (Table 1, Figure 1). If elk foraging distributions represented

by the KNAP90 and GRAS90 samples overlapped in the old-field, the probability of detecting actual elk dietary responses to knapweed removal was reduced.

Diets were compared by first calculating a mean winter diet composition from the five individual diets. The fewest forage taxa with mean percent compositions totalling  $\geq 75\%$  were selected for further analysis. These principal forages were ranked by their percentages in each individual diet, and the five diets were compared using Spearman's rank correlation. Spearman's coefficients were segregated into three diet groups (i.e., KNAP versus KNAP, GRAS versus GRAS, KNAP versus GRAS; Table 1) and grouped coefficients were averaged as an index of diet similarity for comparison among groups. Principal forages were sorted by their occurrence in three habitat categories (i.e., old-field, surrounding native habitats, mixed) and rankings were compared.

### H<sub>0</sub>III: Temporal Trends

Snow depth was measured to the nearest 1 cm in the old-field whenever tracks were counted. Counts of tracks and feeding craters were tested for differences between years using a 1-way analysis of variance. Differences between years were interpreted, in part, by testing track and crater counts (dependent variables) for correlation with snow depth and julian day (independent variables), and multiple linear regression analyses were performed.

Julian day (beginning from 1 December) was presumed to reflect a gradual reduction in the ecological metabolism (Moen 1978) of elk between late-fall and mid-winter, cumulative forage removal, and deteriorating snow conditions (i.e., settling and crusting). Dietary differences between years were examined by comparing Spearman's rank correlation coefficients.

#### H<sub>3</sub>IV: Elk Distribution

I estimated levels of winter elk use on the old-field for comparison with previous estimates by Beall (1974), Hakim (1975) and Lavelle (1986). I recorded all incidental observations of elk in the old-field vicinity. Group size was estimated whenever a group of elk left fresh and individually distinguishable track-sets headed in the same direction. Pellet-groups were counted on the transects in February 1990, and the total was expressed in pellet-groups/ha. A subjective assessment of low, moderate or high elk use was made following the descriptions of Beall (1974), considering all indications of elk presence. Annual aerial surveys of the Threemile elk population (single counts during March or April) continued through this study (J. E. Firebaugh pers. comm.). Differences in mean population size were tested with a t-test. The 1992 flight produced an outlying low count (13) that was omitted.

### Results

Eighteen surveys of elk tracks and feeding craters were accomplished during the first four winters after knapweed removal (Figure 2). A lack of fresh snow prevented more than one survey in 1992. Corresponding fecal samples for diet estimation were not collected that winter.

#### H<sub>3</sub>I: Foraging Activity

I counted 1,803 tracks and 190 feeding craters. Elk walked through adjacent knapweed and grass stands indiscriminately, but pawed only four (2.1%) of the craters in the knapweed stand (Figure 3). Therefore, I rejected H<sub>0</sub>I and concluded that factors associated with knapweed removal attracted elk foraging activity (H<sub>1</sub>I).

#### H<sub>3</sub>II: Diets

Forty-eight forage taxa were identified from a combined 700 elk pellet-groups sampled by Lavelle

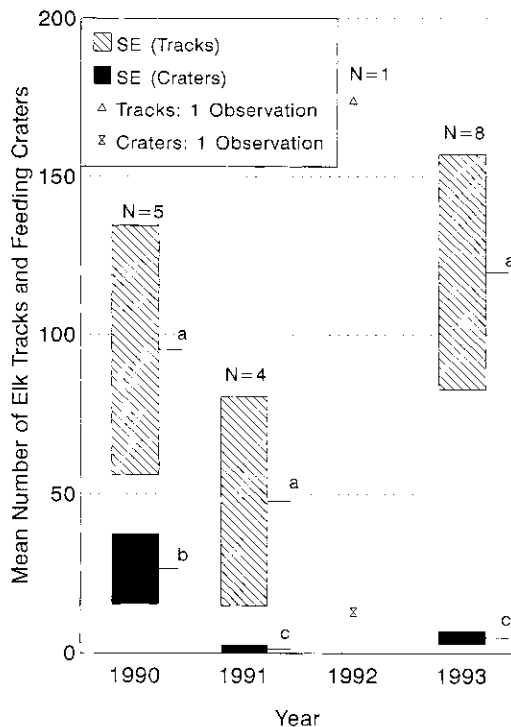


Figure 2. Mean counts (all transects combined) of elk tracks and feeding craters in an old-field on the Threemile Wildlife Management Area. ANOVA (1-way) on tracks by year:  $F = 0.809$ ,  $P = 0.47$ ; ANOVA (1-way) on craters by year:  $F = 4.725$ ,  $P = 0.03$ . Different letters within groups (i.e., tracks or craters) denote significant differences ( $P < 0.10$ ) indicated by Bonferroni test. N = number of surveys.

(1986) and the present study. Thirteen (27.1%) genera comprised >75% of the average winter diet (Table 2). KNAP and GRAS diets (Table 1) generally displayed more similarity within groups than between groups (Table 3). Spearman's coefficients indicated zero correlation between either KNAP diet and the GRAS93 diet, while the GRAS93 and GRAS91 diets displayed the highest correlation (Table 3). Genera characteristic of the old-field (i.e., *Poa*, *Bromus*, *Phleum*) ranked higher in GRAS diets than KNAP diets, while the rankings of widely distributed genera were variable (Table 2). Therefore, I rejected H<sub>0</sub>II and concluded that factors associated with knapweed removal caused measurable shifts in elk winter diets (H<sub>1</sub>II).

#### H<sub>3</sub>III: Temporal Trends

Elk presence in the old-field (i.e., tracks) was consistent through four winters following

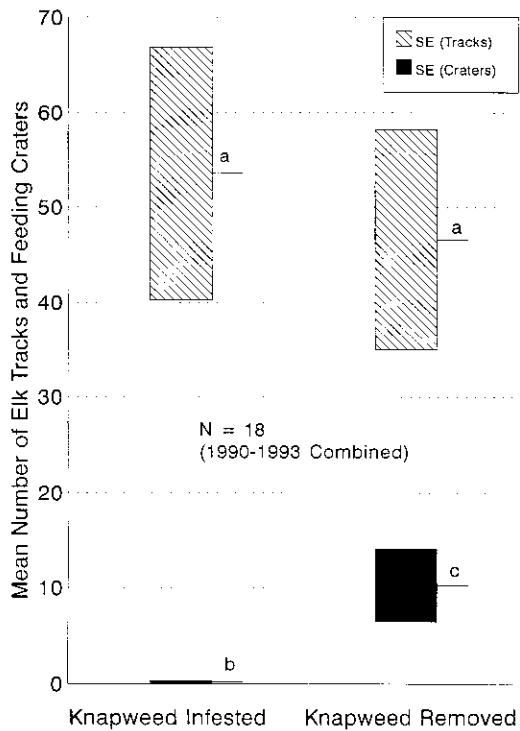


Figure 3. Mean counts of elk tracks and feeding craters by sampling site in an old-field on the Threemile Wildlife Management Area. Different letters within groups (i.e., tracks or craters) denote significant differences ( $P < 0.05$ ). Paired  $t = 0.54$  (tracks) and 2.65 (craters).

knapweed removal (Figure 2). Foraging activity indicated by craters was highest in 1990, and was significantly lower in subsequent winters. During 1990, tracks and craters were not correlated with snow depth, but tracks tended to increase as winter progressed (Table 4). During subsequent years, track counts declined as snow depths increased and winters progressed. The interaction of snow depth and julian day explained 41% of the variation in track counts during 1991-1993. The addition of data from 1990 reduced this explained variation to 8% (Table 4). The GRAS91 and GRAS93 diets displayed more similarity than any other diet comparison, and both diets were relatively dissimilar to GRAS90 (Table 3). Therefore, I rejected  $H_0$ III and concluded that elk responses to factors associated with knapweed removal persisted through the first four winters after knapweed removal, but were more pronounced in the first winter ( $H_a$ III).

#### $H_c$ IV: Elk Distribution

On 31 December 1989, I counted 95 fresh track sets heading west and verified that exactly 95 fresh track sets returned across the old-field. This indicated nearly four times the number of elk encountered during previous studies in the old-field (Table 5). Other measures of elk-use indicated a 170-1,200% increase in this study compared with previous reports (Table 5).

TABLE 2. Principal plant genera in five estimated winter diets of elk on the Threemile Wildlife Management Area (e.g., the KNAP86 diet [Lavelle 1986] pertains to the 1986 winter: Table 1).

Habitat	Diet Composition						
	Combined%		Rank By Winter				
	$\bar{x}$	SD	KNAP86	KNAP90	GRAS90	GRAS91	GRAS93
Old-field grassland primarily							
<i>Poa</i>	12.20	6.49	7	2	1	1	1
<i>Bromus</i>	5.71	3.84	23	12	4	2	4
<i>Phleum</i>	2.58	1.99	23	18	9	10	14
Surrounding rangeland/forest primarily							
<i>Berberis</i>	7.13	4.10	2	5	6	8	9
<i>Carex</i>	6.55	4.53	5	1	3	15	16
<i>Stipa</i>	4.33	3.29	16	13	10	9	3
<i>Artemisia</i>	4.21	3.15	13	4	17	4	12
<i>Balsamorhiza</i>	3.70	1.59	14	7	12	6	10
<i>Pseudotsuga</i>	3.36	3.92	4	22	22	12	11
<i>Calamagrostis</i>	2.89	1.95	23	10	8	22	8
Both old-field and surrounding rangeland/forest							
<i>Festuca</i>	12.25	9.73	1	3	2	5	5
<i>Agropyron</i>	7.25	4.55	12	9	5	3	2
<i>Centaurea</i>	3.91	1.23	8	8	14	7	7
Total	76.07						

TABLE 3. Spearman's correlation coefficients (<sup>a</sup> denotes  $P < 0.05$ , <sup>b</sup> denotes  $P < 0.10$ ) comparing five estimated winter diets of elk on the Threemile Wildlife Management Area (e.g., the KNAP86 diet [Lavelle 1986] pertains to the 1986 winter; Table 1).

Diet	Diet				Average
	KNAP86	KNAP90	GRAS91	GRAS93	
Potentially affected x potentially affected by knapweed removal					
GRAS90			0.335	0.423	
GRAS91				0.610 <sup>a</sup>	
					0.46
Unaffected (KNAP86) x potentially unaffected by knapweed removal					
KNAP90	0.517 <sup>a</sup>				
					0.52
Potentially affected x unaffected or potentially unaffected by knapweed removal					
GRAS90	0.225	0.526 <sup>b</sup>			
GRAS91	0.110	0.308			
GRAS93	-0.005	-0.005			
					0.19

TABLE 4. The influence of snow depth (cm) and julian day (beginning 1 December) on winter counts of elk tracks and feeding craters, as indicated by Pearson correlation coefficients and multiple linear regression, Threemile Wildlife Management Area (<sup>a</sup> denotes  $P < 0.05$ , <sup>b</sup> denotes  $P = 0.07$ ).

Year	N	Dependent Variable	Correlation		Regression	
			Snow	Day	F	R <sup>2</sup>
1990	5	Tracks	0.26	0.54	—	—
		Craters	0.04	0.33	—	—
1991-1993	13	Tracks	-0.44	-0.59 <sup>a</sup>	3.54 <sup>b</sup>	0.41
		Craters	-0.17	-0.06	0.14	0.03
1990-1993	18	Tracks	-0.26	-0.18	0.64	0.08
		Craters	-0.33	0.19	2.08	0.22

TABLE 5. Comparative indications of winter elk presence and abundance on the old-field grassland of Threemile Wildlife Management Area.

Method	Previous Studies	This Study
Subjective assessment	Light elk use, occasionally moderate or no use (Beall 1974). Few elk, minimal use (Lavelle 1986).	Moderate-heavy use, based on the criteria of Beall (1974).
Pellet-group (PG) count	14 PG/ha (Hakim 1975)	184 PG/ha
Largest elk group observed	17 (Lavelle 1986) 11% of N <sup>a</sup> 25, approx. (Beall 1974) 17% of N <sup>b</sup>	68 (18 Jan 1993) 31% of N <sup>c</sup>
Largest elk group, judging from tracks		95 (31 Dec 1989) 43% of N <sup>c</sup>

N<sup>a</sup> = 149 elk estimated in the Threemile population, 1986-1989; N<sup>b</sup> = 148 elk estimated, 1971-1973, by Beall (1974); N<sup>c</sup> = 220 elk estimated, 1990-1994

Annual trend counts of the Threemile elk population averaged 47% higher ( $t = -2.70$ ,  $P = 0.074$ ) during March-April 1990, 1991, 1993 and 1994 ( $\bar{x} = 165$ ,  $SD = 38$ ) than during 1986-1989 ( $\bar{x} = 112$ ,  $SD = 26$ ). Similar methods in comparable cover and terrain in the Elkhorn Mountains detected 74.7% of 87 marked elk (R. M. DeSimone pers. comm.), providing a correction factor to suggest the Threemile population averaged about 220 elk in 1990-1994 and 149 elk in 1986-1989. Beall (1974) used marked animals and multiple census counts to obtain annual estimates of 127-168 elk in the Threemile population in 1971-1973.

Elk numbers and indicators of use in the old-field increased beyond proportions explained solely by the population increase documented during this study. I observed 31-43% of the estimated Threemile population in the old-field, compared with reports equivalent to 11-17% of the population before knapweed removal (Table 5). Therefore, I rejected  $H_0IV$ , and concluded that factors associated with knapweed removal attracted elk to the old-field, presumably from elsewhere within the winter home range of the Threemile population ( $H_aIV$ ).

## Discussion

Factors associated with knapweed removal in the old-field apparently attracted elk numbers equivalent to 14-32% of the Threemile population, in addition to the estimated 11-17% of the population that used the old-field before knapweed removal (Table 5). By definition, this distributional shift toward the old-field ( $H_aIV$ ) also decreased elk-days of use elsewhere across the winter home range. Although otherwise unaffected by knapweed removal, elk remaining in traditionally used habitats away from the old-field may have benefitted from reduced competition for limited resources (e.g., Bartmann et al. 1992). Thus, elk redistribution in response to knapweed removal may have been analogous to a winter population reduction approaching 14-32%. Previous studies have associated changes in population density with changes in the population dynamics of elk (Buechner and Swanson 1955) and red deer (*C. e. scoticus*, Clutton-Brock et al. 1982:259-285).

Moreover, knapweed removal expanded foraging options for the estimated 31-43% of the elk population (Table 5) which used the old-field ( $H_aI$ ). A corresponding dietary response to fac-

tors linked with knapweed removal was detected in all three winters ( $H_aII$ ). This dietary response was indicated by fecal analysis despite high environmental variability which may have overwhelmed this study's power to detect more subtle dietary changes of potential biological significance (White 1983). Environmental variability was high because: (1) knapweed removal modified only about 5% (i.e., old-field) of the winter home range of free-roaming elk, (2) few forage taxa occurred in the old-field compared to the remainder of the winter home range, and (3) plant fragments in feces collected in the old-field may have been ingested at distant feeding sites several days before defecation (Nelson and Legee 1982). I infer high biological significance from the fact that a dietary response attributable to knapweed removal could be distinguished from the influences of these uncontrolled variables. Likewise, Wickstrom et al. (1984:1299) concluded that management practices affecting vegetation on winter ranges are likely to have profound impact on ungulate foraging efficiency during the season when energy balance is especially critical.

The KNAP90 and GRAS90 diets were rank correlated (Table 3). This was an expected result of sampling both diets from the same population during the same winter (Table 1), and did not diminish the importance of observed differences between these diets which were attributed to factors associated with knapweed removal (Table 2). Further, the significant rank correlation between the KNAP90 and KNAP86 diets, and a lack of correlation between the GRAS90 and KNAP86 diets (Table 3), promoted confidence in the KNAP86 diet as a valid baseline for assessing dietary changes linked with knapweed removal. Therefore, the purpose for estimating the KNAP90 diet was served.

Only one treatment site and one control site were compared. Therefore, this study lacked replication, which precluded the use of inferential statistics to test for treatment effects (Hurlbert 1984). The t-test in Figure 3 indicated that crater counts differed between sites while track counts did not. From this, I concluded that elk foraged more on the treated site than on the control site, though they walked through both sites indiscriminately. This, considered with the other results of this study, led me to subjectively conclude that factors associated with knapweed removal (i.e., the treatment itself) caused the observed foraging

response. Replication was sacrificed to evaluate a treatment of sufficient size for assessing management applications while simultaneously confining environmental variation to that found within the range of a single elk population. Replicated experiments, as well as observational studies such as this one, are needed to advance ecological understanding (Eberhardt and Thomas 1991).

Factors associated with knapweed removal were most attractive to foraging elk in 1990 (H<sub>III</sub>, Figure 2). This initial attraction appeared to override the effects of snow depth and winter duration which influenced foraging activity in 1991-1993 (Table 4). Knapweed removal may have attracted elk because: (1) knapweed was removed, (2) grass standing crop increased, and/or (3) forage quality characteristics of the grasses improved. Knapweed and grass standing crops were consistent across all winters after knapweed removal and could not explain a higher attraction in 1990. However, forage quality may have been higher in 1990 due to: (1) a short-term fertilizer effect caused at the time of treatment by a release of nutrients previously occupied by living knapweed plants (Harvey and Nowierski 1989), and/or (2) a one-time occurrence of abundant green grass on the winter range.

More grass litter was present in the old-field in 1991-1993, but probably did not explain the abrupt drop in foraging activity observed in 1991. Jourdonnais and Bedunah (1990) observed less elk feeding use of rough fescue (*F. scabrella*) plants with dense standing litter. While rough fescue produces dense tufts of persistent standing litter, the nontufted grasses prevalent in the old-field (e.g., bluegrasses and bromes) did not. By ocular estimate, elk consumed about 35% of the grass standing crop on the transects before 25 February 1990, and the remaining unconsumed foliage tended to flatten, presenting no apparent obstruction to elk feeding on current year's growth in the winter of 1991.

The effects of knapweed removal appeared to continue attracting elk foraging activity and influencing winter diets in 1991-1993 (Figure 2; Tables 2, 3, and 5). Prior to knapweed removal, a high density of coarse, persistent, knapweed stems may have deterred elk from grazing the scattered grass plants in the old-field, comparable to the effect of standing dense litter on elk use of rough fescue (Jourdonnais and Bedunah 1990). Addi-

tionally, grass production gains concurrent with knapweed removal may have increased winter foraging efficiency. Wickstrom et al. (1984) reported that dry matter intake rate decreased when elk grazed grass stands with forage biomass levels below a threshold of about 1,500 kg/ha, and they concluded it was unprofitable for elk to graze grass swards of low productivity, regardless of digestibility. Applying their results to the present study, the increase from about 700 kg/ha grass to 1,600 kg/ha (Carpenter 1986) caused by picloram treatment may have exceeded a production threshold important in the foraging energetics of wintering elk.

The foraging response of elk might have been stronger in 1991-1993 if native bunchgrasses were more abundant in the old-field. Although bluegrasses comprised 18% of the winter elk diet in the Elkhorn Mountains, Gordon (1968) reported that elk did not use cured bluegrass foliage. The cured foliage of Idaho fescue and bluebunch wheatgrass were the primary winter foods reported by Gordon (1968). Likewise, Threemile elk were attracted to the bluegrass dominated old-field when grasses were predominately green in 1990, but foraged less in the old-field when bluegrasses were predominately cured in 1991-1993.

## Conclusions and Recommendations

Elk populations in Montana are at twentieth century highs (Firebaugh 1993), coincident with the increase and spread of knapweed (Lacey 1989). Although existing habitat could support more elk, lower population objectives are necessary for compatibility with competing human uses of the land (Wildl. Div., Elk Manage. Plan, MDFWP, Helena, 1992). Thus, the question of whether existing knapweed infestations on elk winter ranges limit ecological carrying capacity is somewhat academic when elk numbers are limited to a lower economic carrying capacity, as defined by Caughley (1979).

Nevertheless, the results of this study are pertinent to elk management in two respects. First, continued spread of knapweed beyond current distributions, and increased knapweed densities within existing stands, should concern managers of grassland winter ranges who strive to maintain the current productivity of associated elk herds. Second, removal or thinning of existing knapweed stands in favorable foraging habitats may attract

elk, potentially yielding similar habitat and herd enhancement results as fertilizing, burning, and prescribed cattle grazing (Rowland et al. 1983, Skovlin et al. 1983, Jourdonnais and Bedunah 1990, Frisina 1992).

It is unknown if the elk foraging response in the old-field was representative of the response managers should expect from knapweed removal on typical bunchgrass winter ranges. Recovery rates of native rangelands may be depressed by historical use (Willms et al. 1985), which would remain a factor regardless of knapweed removal. Extrapolating the results of the present study, knapweed removal would elicit the largest foraging response where preexisting densities of both knapweed and preferred forage grasses were high. Further, at least a portion of the elk response to knapweed removal in the old-field was likely attributable to a short-term forage quality increase in the first winter following picloram treatment. The coincidence of massive knapweed mortality with adequate rainfall was probably an impor-

tant determinant of the observed forage and elk response in the first winter. Managers hoping to replicate these conditions should apply picloram or other appropriate herbicides as soon as the range becomes snow-free in spring to take full advantage of available moisture in the first growing season.

### Acknowledgements

I am grateful to J. E. Firebaugh for project supervision, critical review, and enthusiastic support of the publication effort; G. R. Baty for exceptionally thorough and helpful reviews and discussions of two draft manuscripts; H. E. Jorgensen, D. J. Bedunah, S. D. Rose, B. B. Davitt, M. R. Frisina, and C. L. Marcum for their advice during the study and critical reviews of draft manuscripts; R. E. Henderson for computer assistance; and an anonymous reviewer for helpful comments. This study was funded by the Montana Department of Fish, Wildlife and Parks.

### Literature Cited

- Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. *Wildl. Monogr.* 121.
- Beall, R. C. 1974. Winter habitat selection and use by a western Montana elk herd. University of Montana, Missoula. Ph.D. Dissertation.
- Bedunah, D., and J. Carpenter. 1989. Plant community response following spotted knapweed (*Centaurea maculosa*) control on three elk winter ranges in western Montana. In P. K. Fay, and J. R. Lacey (eds.) Proc. 1989 Knapweed Symp., Montana State University, Bozeman. Pp. 205-212.
- Buechner, H. K., and C. V. Swanson. 1955. Increased natality resulting from lowered population density among elk in southeastern Washington. *Trans. North Am. Wildl. Conf.* 20:560-567.
- Carpenter, J. L. 1986. Responses of three plant communities to herbicide spraying and burning of spotted knapweed (*Centaurea maculosa*) in western Montana. University of Montana, Missoula. M.S. Thesis.
- Caughley, G. 1979. What is this thing called carrying capacity? In M. S. Boyce, and L. D. Hayden-Wing (eds.) *North American Elk: Ecology, Behavior and Management*, University of Wyoming Press, Laramie. Pp. 2-8.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. *Red Deer: Behavior and Ecology of Two Sexes*. The University of Chicago Press, Chicago.
- Eberhardt, L., and R. C. Van Etten. 1956. Evaluation of the pellet group count as a deer census method. *J. Wildl. Manage.* 20:70-74.
- Eberhardt, L. L., and J. M. Thomas. 1991. Designing environmental field studies. *Ecol. Monogr.* 61:53-73.
- Fay, P. K., and J. R. Lacey (eds.). 1989. Summary of the "research needs" meeting. In Proc. 1989 Knapweed Symp., Montana State University, Bozeman. P. 230.
- Firebaugh, J. 1993. Elk status report—Montana. In J. D. Cada, J. G. Peterson, and T. N. Lonner (comps.) Proc. West. States and Prov. Elk Workshop., Montana Department of Fish, Wildlife and Parks, Bozeman. P. 8.
- Frisina, M. R. 1992. Elk habitat use within a rest-rotation grazing system. *Rangelands* 14:93-96.
- Gordon, F. A. 1968. Range relationships of elk and cattle on elk winter range. Crow Creek, Montana. Montana State University, Bozeman. M.S. Thesis.
- Hakim, S. A. 1975. Range condition on the Threemile Game Range in western Montana. University of Montana, Missoula. M.S. Thesis.
- Harvey, S. J., and R. M. Nowierski. 1989. Spotted knapweed: allelopathy or nutrient depletion? In P. K. Fay, and J. R. Lacey (eds.) Proc. 1989 Knapweed Symp., Montana State University, Bozeman. P. 118.
- Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54:187-211.
- Jourdonnais, C. S., and D. J. Bedunah. 1990. Prescribed fire and cattle grazing on an elk winter range in Montana. *Wildl. Soc. Bull.* 18:232-240.
- Lacey, C. 1989. Knapweed management: a decade of change. In P. K. Fay, and J. R. Lacey (eds.) Proc. 1989 Knapweed Symp., Montana State University, Bozeman. Pp. 1-6.
- Lavelle, D. A. 1986. Use and preference of spotted knapweed (*Centaurea maculosa*) by elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) on two winter ranges in western Montana. University of Montana, Missoula. M.S. Thesis.

- Lolo National Forest. 1991. Noxious weed management. Final Environ. Impact Statement. Missoula, Montana.
- Lyon, L. J., and A. L. Ward. 1982. Elk and land management. In Thomas, J. W., and D. E. Towell (eds.) *Elk of North America—Ecology and Management*. Stackpole Books, Harrisburg, Pennsylvania. Pp. 442-477.
- Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. *J. Wildl. Manage.* 42:715-738.
- Moors, G. B. 1986. Relationship of critical environmental factors to the success of spotted knapweed (*Centaurea maculosa*) in western Montana. University of Montana, Missoula, M.S. Thesis.
- Nelson, J. R., and T. A. Leege. 1982. Nutritional requirements and food habits. In Thomas, J. W., and D. E. Towell (eds.) *Elk of North America—Ecology and Management*. Stackpole Books, Harrisburg, Pennsylvania. Pp. 322-367.
- Rowland, M. M., A. W. Alldredge, J. E. Ellis, B. J. Weber, and G. C. White. 1983. Comparative winter diets of elk in New Mexico. *J. Wildl. Manage.* 47:924-932.
- Skovlin, J. M., P. J. Edgerton, and B. R. McConnell. 1983. Elk use of winter range as affected by cattle grazing, fertilizing, and burning in southeastern Washington. *J. Range Manage.* 36:184-189.
- Spoon, C. W., H. R. Bowles, and A. Kulla. 1983. Noxious weeds on the Lolo National Forest: a situation analysis staff paper. USDA For. Serv., Missoula, Montana. 33 p.
- Stewart, D. R. M. 1967. Analysis of plant epidermis in faeces: a technique for studying the food preferences of grazing herbivores. *J. Appl. Ecol.* 4:83-111.
- Tyser, R. W., and C. H. Key. 1988. Spotted knapweed in natural area fescue grasslands: an ecological assessment. *Northw. Sci.* 62:151-159.
- White, R. G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. *Oikos* 40:377-384.
- Wickstrom, M. L., C. T. Robbins, T. A. Hanley, D. E. Spalinger, and S. M. Parish. 1984. Food intake and foraging energetics of elk and mule deer. *J. Wildl. Manage.* 48:1285-1301.
- Willms, W. D., S. Smoliak, and J. F. Dormaar. 1985. Effects of stocking rate on a rough fescue grassland vegetation. *J. Range Manage.* 38:220-225.

Received 11 March 1995

Accepted for publication 25 October 1995