Predation Risk and Elk-Aspen Foraging Patterns

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***Abstract**—Elk-aspen foraging patterns may be influenced by cover type, distance from roads or trails, the type of user on road or trail (park visitor, human hunter, or predator), and two general states of aspen condition (open-grown or thicket). Pellet group and browse utilization transects in the Canadian Rockies showed that elk were attracted to roads used by park visitors and avoided by wolves, and that elk possibly avoided aspen and conifer patches near backcountry trails used by wolves. In high predation risk landscapes, aspen stands were dense, lightly browsed, and rarely entered by elk. As risk decreased, elk density and aspen browsing increased proportionally faster on edges of aspen stands compared to the interior of aspen stands. In low risk landscapes, edge and interior plots were intensively used, and stands had a low density of heavily browsed stems. Regeneration of aspen stands likely requires low densities of risk-sensitive elk.*

Introduction

Trembling aspen (*Populus tremuloides*) is an indicator species for low elevation, montane ecoregions in Rocky Mountain national parks (Achuff et al. 1996; White et al. 1998a). Aspen stands are typically long-lived clones, regenerated by frequent fires (Mitton and Grant 1996; Kay 1997a). In the Rocky Mountains, aspen communities are second only to riparian zones for species richness (DeByle 1985a; Finch and Ruggiero 1993). Aspen stands historically had a range of age and size classes (Gruell 1979; Houston 1982). However, since the late 1800s to 1930s (depending on the location), new aspen stems have rarely grown to heights >1 m on elk (*Cervus elaphus*) winter ranges in several national parks and wildlife refuges (Packard 1942; Cowan 1947; White et al. 1998a) including Yellowstone National Park (Houston 1982; Kay 1990; Romme et al. 1995), near Jackson Hole, Wyoming (Gruell 1980; Boyce 1989), in Rocky Mountain National Park, Colorado (Olmsted 1979; Baker et al. 1997), Banff and Jasper National Parks in Alberta (Kay et al. 1999), and Yoho and Kootenay National Parks in British Columbia (Kay 1997b).

The factors responsible for aspen decline (figure 1) remain controversial (Kay 1997a; Huff and Varley 1999) but there are three broad theories for long-term aspen condition (Keigley 1997; Singer et al. 1998):

1. Heavily browsed aspen stands persisted under intense herbivory by abundant, food-regulated elk (Romme et al. 1995; Boyce 1998). This is termed ecological carrying capacity (Caughley 1976, 1979). The current decline of aspen is simply a return to long-term conditions as elk populations recover from overhunting by humans during the late 1800s. Episodic events such as a combination of cool-moist climate and fire could result in pulses of aspen stems periodically reaching tree size (Romme et al. 1995).

2. Aspen was historically vigorous, lightly browsed, and coexisted with moderate to high densities of elk, but has recently degenerated due to the combination of herbivory, fire suppression, and possibly climate change (Gruell 1979, 1980; Houston 1982).

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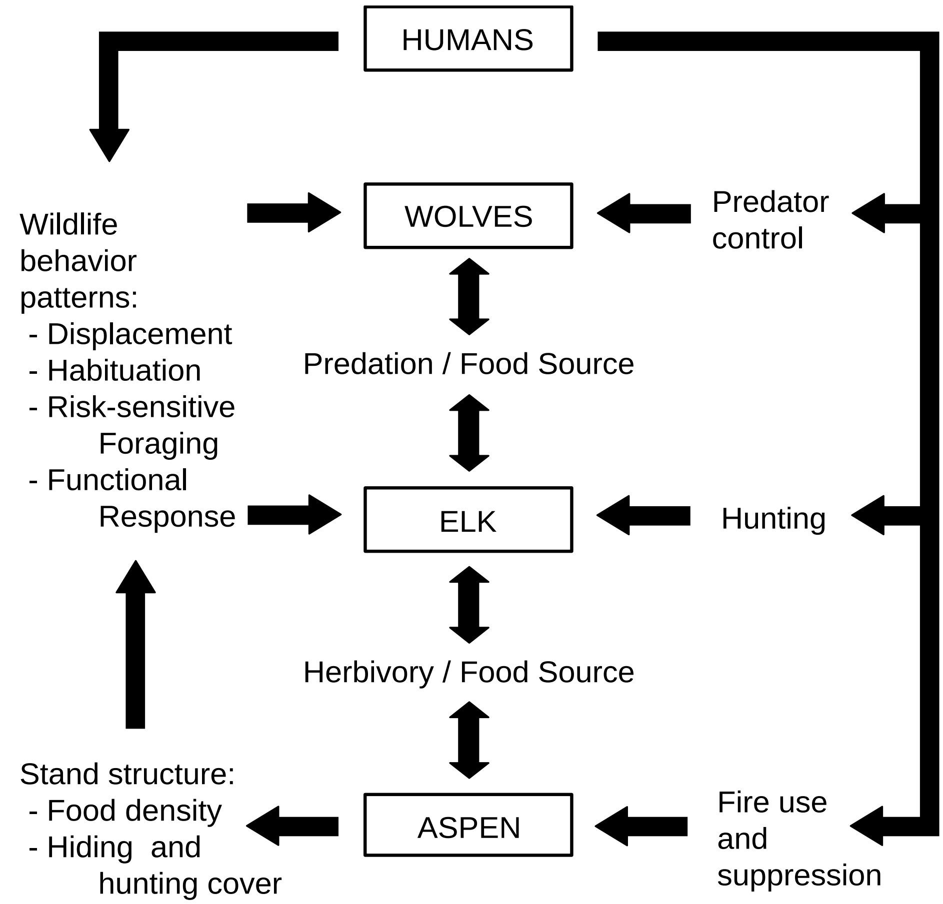

Figure 1—A trophic-level model for interactions between humans, wolves, elk, and aspen.

3. Aspen persisted under conditions of low elk density and herbivory (Packard 1942; Cowan 1947; Olmsted 1979), maintained by intense predation on elk from humans, wolves, and other carnivores (Kay 1990, 1998; White et al. 1998a,b).

Analysis of aspen abundance, fire effects, and historical and current elk distribution patterns in Rocky Mountain national parks (Kay 1990; White et al. 1998a; Ripple and Larsen 2000) provided support for hypothesis 3; recent (since about 1900) reductions of predation rates on elk have resulted in increased elk herbivory on aspen. If this hypothesis is valid, predators could influence the elk-aspen herbivory interaction in two ways: first, the lethal effect of killing elk thus reducing elk density and herbivory; and second, the nonlethal effects where predation risk alters elk behavior in ways that reduce herbivory on aspen (figure 1). Direct effects on aspen due to general elk density and browsing levels are significant (Olmsted 1979; Kay 1990; White et al. 1998a). However, nonlethal consequences of predation risk are also important influences on animal foraging behaviors (Lima and Dill 1990; Lima 1998; Kie 1999). After reviewing historical conditions in Yellowstone National Park, Ripple and Larsen (2000) hypothesized that elk behavioral responses to wolves could have influenced aspen herbivory levels in riparian areas of Yellowstone National Park.

In this study we explored two possible effects of predation risk on elk foraging patterns on aspen during winter (October through March): (1) effects of travel routes used by predators (humans and wolves) on elk habitat use; and (2) effects of aspen stand structure (thicket versus open-grown) and predation or hunting risk on elk foraging behavior. We test the general hypothesis that these nonlethal effects are important determinants of aspen condition.

Theory and Predictions

Plants and large mammalian herbivores have two-way interactions (Noy-Meir 1975; Caughley 1976; Schmitz and Sinclair 1997). Plants provide food, shelter, and cover for herbivores and their predators. Herbivores alter plants or their habitats directly by feeding and trampling on plant parts, and indirectly by nutrient additions through defecation and urination (Hobbs 1996; Augustine and McNaughton 1998).

Predation Theory

Elk browsing rates on aspen appear to increase with decreasing stem density (Debyle 1985a,b; Kay and Wagner 1996; C. White, unpublished data). In predation theory, this is described as a Type 2 functional predation response (Holling 1959; Taylor 1984). Type 2 functional responses are common in simple one predator-one prey herbivory systems (Lundberg and Dannell 1990). However, in the multi-prey, elk-aspen situation, where numerous alternative plant forage species are readily available, the Type 2 response indicates that aspen is highly preferred by elk. High priority prey will be used even at low densities, and may have few refuges from predation (Pech et al. 1995; Sinclair et al. 1997; Augustine and McNaughton 1998). The high value of aspen as ungulate forage has been noted in other studies (e.g., Nelson and Leege 1982; Hobbs et al. 1982; Dannell et al. 1991). DeByle (1985b) described increased browsing rates when aspen stem densities are low. In Yellowstone National Park, Kay and Wagner (1996) found that ongoing high herbivory had reduced most aspen clones to low numbers of heavily browsed stems, and for approximately one-third of aspen stands shown in early photographs, both the stems and roots appeared to have completely died out.

Olmsted (1979) estimated that the twig browsing threshold between viable and declining aspen stands occurred when approximately 30% of current annual growth was browsed. Theoretically, the Type 2 functional response will cause this threshold to be a curved isoline for a range of aspen and elk densities (figure 2). At high aspen stem densities, per elk twig consumption declines, and

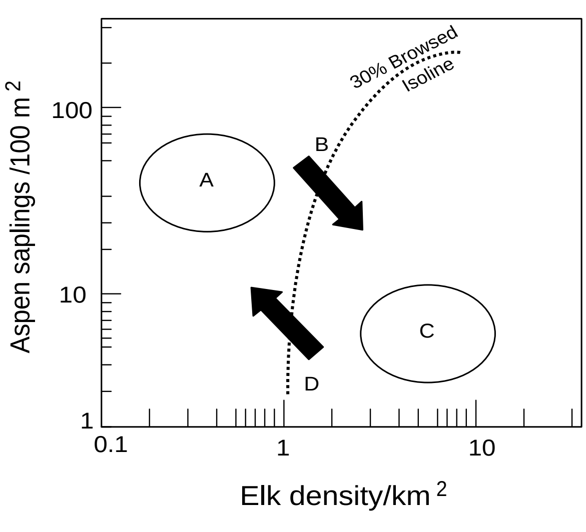

Figure 2—A state and transition model of aspen sapling density as a function of elk density. Stands near A have abundant aspen saplings, and stands near C have few saplings. Transitions between states occur near the 30% browsed isoline and are shown by arrows at B and D.

aspen can sustain a higher density of elk. The curvilinear response could result in elk-aspen herbivory being approximated by a state-and-transition type model (e.g., Noy-Meir 1975; Walker et al. 1981; Westoby et al. 1989). Aspen would have two general alternative states (Gruell 1980; Kay 1990; White et al. 1998a): dense sapling (stems 2 to 6 m height) thickets (around A in figure 2), and few saplings (around C). The transitions (at B and D) between states could be rapid but have different pathways and mechanisms depending on the direction of change. At high aspen sapling density (A), elk density could be moderate (e.g., 1 to 3 elk/km^2; White 1998a) with aspen sapling survival because the per capita elk foraging rate is lower in denser sapling stands. The transition toward few, heavily browsed aspen saplings probably occurs around B at 3 to 5 elk/km^2, or 1 to 2 elk pellet groups/100 m^2 (White et al. 1998a; C. White, personal observation). At low aspen sapling densities (C), per elk foraging rates on suckers and saplings would be high (DeByle 1985a,b). Elk densities might have to be <1 elk/km^2 (<1 pellet group/100 m^2) for stands to cross the transition at D toward more abundant aspen saplings (White et al. 1998a).

In traditional predation theory (Holling 1959), a Type 2 response is attributed to the limitations imposed by handling time, which for herbivores is a complex set of interactions between the competing activities of searching, biting, cropping, and chewing (Spalinger and Hobbs 1992). However, an alternative explanation is reduced herbivore foraging rates when higher vegetation density increases predation risk (Fritz 1992; Hare 1992).

Risk-Sensitive Foraging

Three-level trophic communities (predators-herbivores-plants) are influenced by multi-way interactions (Price et al. 1980; Hunter and Price 1992; Fryxell and Lundberg 1997; Krebs et al. 1999) that may change herbivore abundance or behavior and hence regulate community structure (Hairston et al. 1960). Predation-sensitive foraging models are based on tradeoffs between the benefits of energy intake and the costs of a shortened reproductive life due to predation (Sih 1987; Lima and Dill 1990; Lima 1998). Successful herbivores should utilize their environments in ways that balance safety with feeding. In situations where predation risk is low, animals should forage in high-resource habitats where energy intake is maximized. If predation risk is high in these habitats, however, safer locations with less forage availability may be used. In situations where low-resource habitats are risky, animals should concentrate in better habitats until resources are greatly depleted (Fryxell and Lundberg 1997). Where three-level trophic systems have coevolved, development of plant structures that increase the risk of predation on herbivores, thus providing "enemy-free space" with low herbivory, could increase plant fitness (Price et al. 1980; Jeffries and Lawton 1984; Fritz 1992).

Elk and Predator Behavior Patterns

Previous research provides several areas of knowledge for potential elk-aspen foraging patterns under predation risk. First, studies of elk habitat use in the Rocky Mountains report a general cover type preference of grassland > aspen > conifer (Collins and Urness 1979; Houston 1982; Holroyd and Van Tighem 1983). Numerous studies rank aspen as a highly favored elk forage species (Nelson and Leege 1982). Aspen twigs, leaves, and bark have relatively high concentrations of important nutrients (Jelinski and Fisher 1991), and at northern latitudes they are a valuable food source for elk, particularly during winter (Hunt 1979; Rounds 1979). Second, wolves (*Canis lupus*) and humans, two of elk's dominant predators (Cowan 1947; Huggard 1993a; Kay 1994), have consistent travel corridors in the Rocky Mountains. Both species usually follow valley bottom trails or lightly used roads, and in winter they may utilize ice-covered streams (Carbyn 1974; Huggard 1993a; Paquet et al. 1996; Kunkel 1997). Wolves prefer trails with snow depths <20 cm (Huggard 1993b) and often follow routes packed or plowed by humans (Paquet et al. 1996). Third, in areas with low herbivory, recently disturbed aspen stands and the edges of older stands often have dense patches (<1 m spacing) of young stems (DeByle 1985a; Shepperd and Fairweather 1994). These thickets could provide cover for stalking carnivores such as cougar (*Felis concolor;* Kunkel et al. 1999) and impede elk escape if predator attack does occur (e.g., Lima 1992). Finally, an important elk defense against predation may be group foraging in open areas where stalking predators such as cougars are more detectable (Kunkel et al. 1999) and elk have running room to escape (Geist 1982). Also, in the Rocky Mountains, snow depths are often lower in wind-swept open areas, which increase elk's ability to forage (Skovlin 1982; Lyon and Ward 1982) and escape predation (Huggard 1993b).

These previous observations suggest that patterns of elk and predator foraging could occur in spatially nested scales (Senft et al. 1987; Bailey et al. 1996), which for this study we characterize as landscapes, corridors, and patches (figure 3). At a macro-scale (>10 km^2), human land-use structures elk habitats into high-predation risk and low-predation risk landscapes. High risk landscapes could have wolves and human hunters. A low risk landscape could be a busy national park where elk are unhunted and predators are few such as the Bow Valley in Banff National Park, Alberta, or Rocky Mountain National Park in Colorado (White et al. 1998a). The landscape level defines general elk population densities and behavior patterns. At the meso-scale corridor level (1 to 10 km^2), trails, roads, and streams provide corridors for human and predator travel. Depending on the rates of human hunting and predator control, elk and predators may either be attracted to or avoid corridors near these travel routes (Lyon 1979; Dekker et al. 1995; Ripple and Larsen 2000). At the micro-scale (0.01 to 1 km^2) patch level, macro- and meso-scale phenomena determine

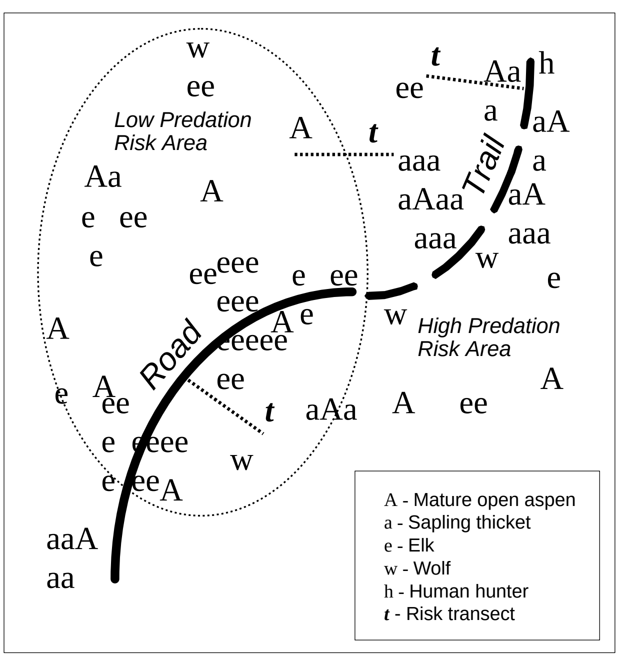

Figure 3—A spatial model of elk-aspen distribution patterns at 3 scales: macro-scale (high and low predation risk landscapes), meso-scale corridors (distance from road or trails), and micro-scale (aspen stand habitat patches). The stylized locations of the predation risk transects used in this study are shown with dotted lines.

differential elk foraging strategies within patches. For this study, these patch types include grass, aspen and conifer cover types, or dense aspen thickets versus open stands.

Predictions on Effects of Human and Predator Travel Routes

Given predator travel patterns, we predicted that in high predation landscapes (figure 3), elk will trade off food availability for safety, and forage relatively less in corridors next to trails used by wolves and humans than at distances farther from trails (table 1). For example, in studies of human-hunted elk, significant reduction in elk use (>60%) was found up to at least 500 meters from roads in Montana (Lyon 1979), and within 200 meters from roads in Colorado (Rost and Bailey 1979). In contrast, in low predation risk landscapes, elk are often unhunted and human-habituated (White et al. 1998a). They should be attracted to corridors next to busy roads avoided by wolves (Dekker et al. 1995; Paquet et al. 1996). The differential effect of trails or roads on elk use should be evident as an interaction (table 1) between the effects of landscape type (high or low risk) and distance from road or trail (close, moderate, or far).

At the patch level, nested within corridors, we expected a response of elk use to interactions between region, distance from road or trail, and cover type (table 1). As risk increases, elk selectivity for grassland cover, which is most preferred by elk and could offer the safest foraging areas, should increase while low resource-value conifer habitats should most rapidly be abandoned (Houtman and Dill 1998; Fryxell and Lundberg 1998). Aspen habitats, with intermediate value, should have intermediate trends.

Predictions on Effects of Aspen Stand Structure

At the micro-scale level, elk use of aspen patches in comparison to the surrounding matrix of grassland can be viewed as an integrator of local habitat preference, competition, and predation risk (Brown 1988). In landscapes with high predation risk, low elk density, and abundant forage in grasslands (A in figure 2), we predicted that dense aspen sapling thickets, which could provide cover for predators, would rarely be entered by risk-sensitive elk (table 2). Under low browsing pressure, thickets persist because regeneration of aspen remains continuous at the edge of clones, thereby inhibiting herbivore use. If predation risk decreases and elk density increases (toward the 30% twigs browsed isoline between B and D), elk use should increase most rapidly in grasslands next to aspen. If thickets continue to discourage elk use, this will create a maximum difference in elk use between grasslands and aspen. As elk densities increase

Table 1—Predictions for elk corridor and patch use for high predation and low risk predation landscapes at three distances from trails used by predators.

Distance from main valley bottom trail or highway	Landscape risk: High predation risk with trail used by wolves	Landscape risk: Low predation risk with busy highway avoided by wolves
Close (<100 m)	Lowest Grass >>> Aspen >>> Conifer	Highest Grass > Aspen > Conifer
Moderate (100 to 500 m)	Moderate Grass >> Aspen >> Conifer	Moderate Grass >> Aspen >> Conifer
Far (500 to 1,000 m)	Highest Grass > Aspen > Conifer	Lowest Grass >>> Aspen >>> Conifer

Table 2—Predictions for elk patch use and browsing rates for grasslands on the edge of aspen stands, and the interior of stands for three predation risk levels.

Predation risk	Relative elk habitat use and browsing rates	Remarks
High	Edge > Interior	Heavily hunted area, or area near trail used by wolves, elk use low in both edge and interior patches
Moderate	Edge >> Interior	Elk use increases first at edge of aspen stands
Low	Edge = Interior	Aspen thickets removed, elk use all areas

farther in low risk landscapes (toward C), the risk-sensitive foraging tradeoff should result in strong pressure for elk to utilize areas within aspen thickets. Higher elk browsing of thickets will in turn, over time, reduce thicket density. Where thickets are removed, elk should have similar use levels in aspen and grassland cover types.

Table 3—Study areas and data collected in each area.

Study area	Road and trail pellet count transects on risk gradients	Paired edge: interior aspen stand transects on risk gradients	Model thickets
Jasper National Park-Willow Creek	5 transects—running from 500 to 800 m from trail to edge of trail, plus >15 km of wolf scat counts on trails	1 transect—running from 600 m away from trail to the trail in Mud Creek meadow	
Ya Ha Tinda Ranch		1 transect—running across ranch boundary from east at Eagle Creek	
Banff National Park-Bow Valley	5 transects—running from 500 to 1,000 m from Trans Canada Highway to edge of highway fence, plus >15 km of wolf scat counts on trails	1 transect—running across east park boundary near Harvey Heights, Alberta	5—located from 0.3 to 5 km from Banff townsite at Recreation Grounds, Hoodoos, Golf Course and Indian Grounds and Duthill
Bow Valley Provincial Park		1 transect—running from Kananaskis River to center of park at Many Springs Pond	
Kananaskis Golf Course		1 transect—running from clearcuts east of Boundary Ranch to powerline through Golf Course	

Study Areas and Methods

We tested predictions by evaluating elk use (indexed by pellet counts) and browsing effects in aspen stands and adjacent grasslands and forests on five valley-bottom elk winter range areas of the Canadian Rockies in Alberta (table 3). The Jasper-Willow Creek area is a ≈30 km^2 area in Jasper National Park where wolf predation on elk has been frequently observed (Carbyn 1974; Dekker et al. 1995). In 1999, about 20 to 40 elk utilized the area during winter (Bradford, personal communication). These elk may periodically leave the park onto Alberta provincial lands where they are hunted during fall hunting seasons or year-round by Treaty Indians (Dekker et al. 1995). The Ya Ha Tinda Ranch is a ≈100 km^2 area along the Red Deer River adjacent to Banff National Park where approximately 1,000 to 2,000 elk winter on grasslands within 3 to 5 km of the ranch buildings (Morgantini 1995). During the study, wolf use was relatively high in areas farther away from the ranch and bull elk were hunted during a fall rifle-hunting season. Three study areas (Kananskis Golf Course, Bow Valley Provincial Park, Banff-Bow Valley) were in the lower Bow Valley on Alberta provincial lands and in Banff National Park. The Bow Valley has several areas of different wolf and human predation rates on elk (Paquet et al. 1996). The ≈100 km^2 Banff-Bow Valley area is bisected by a fenced highway and provides habitat for over 500 elk. Near Banff townsite, human-caused mortality rates on elk (from roads and the railroad) were 2% per year on roads and the railroad, and wolves took <4% per year (Paquet et al. 1996; Woods et al. 1996). Elk also concentrated on unhunted zones in Bow Valley Provincial Park, 50 km east of Banff, and the Kananaskis Golf Course complex, 60 km southwest of Banff (Alberta Environment Protection files, Canmore Office).

All study areas are in the montane or lower subalpine ecoregions of the Canadian Rockies (Strong 1992). Vegetation cover is predominantly lodgepole pine (*Pinus contorta*) forests interspersed with stands of trembling aspen, Douglas-fir (*Pseudotsuga menziesii*), white spruce (*Picea glauca*), and grass meadows with shrub birch (*Betula* spp.) and willow (*Salix* spp.) shrublands (Achuff and Corns 1982; Archibald et al. 1996; Beckingham et al. 1996). The study areas have a continental climate with peak precipitation in June and winter snow depths generally less than 50 cm (Holland and Coen 1982).

Ungulate and Wolf Habitat Use

We used pellet and scat counts on belt transects to index relative winter habitat use by wolves and ungulates (Neff 1968; Edge and Marcum 1989). Elk defecate most frequently when active, so pellet counts are likely biased toward areas where elk are feeding or moving as opposed to bedding (Collins and Urness 1979). Transects were measured in April and May, immediately after the winter snowpack melted. We evaluated wolf and elk habitat use by cover type and distance from trails and roads (table 3) at Jasper-Willow Creek (low human use, high wolf use, low elk density) and Banff-Bow Valley area (high human use, low wolf use, high elk density). From air photographs, we identified five transect locations (figure 3) perpendicular to the main valley bottom trails (Jasper area) and the Trans Canada Highway (Banff area) where a mix of aspen, conifer, and grassland habitat patches was found at 10 to 100 m, 100 to 500 m, and 500 to 1,000 m from the road or trail. Aspect and elevation were relatively similar along the transect. On the air photographs, we selected locations for five 2 x 50 m plots in each cover type at each of the three distances from the trail or road for each transect. All scats and ungulate pellet groups with centers within plots were counted by species.

We used a factorial analysis (2 study areas x 3 cover types [grass, aspen, conifer] x 3 distances from trail/road [close, moderate, far]) to test for main and interaction effects on the elk pellet group counts. Although frequency count data typically follow a negative binomial distribution, simulations by White and Bennetts (1996) showed that analysis with ANOVA is relatively robust to violations of normality. We minimized the effects of violations of parametric assumptions (normal distribution and equal variance) by balancing sample sizes for groups (Underwood 1997), comparing results of alternative data transformations of pellet counts on normal probability plots (Zar 1996), and using the square root transformation ($\sqrt{[\text{count} + .5]}$).

We tallied all wolf scats within 1 m of the main trail centers in the Willow Creek area of Jasper National Park for 3 years (1997, 1998, 1999), on side trails in Willow Creek for 1 year (1999), and on side trails near the Trans Canada Highway in the Banff-Bow Valley for 2 years (1998, 1999). Each trail was surveyed once in April or May, immediately after snowmelt. Trail distances by cover type were measured by wheel-odometer.

To evaluate effects of aspen stand structure and predation risk on elk habitat use (table 2), we identified five transects (table 3) across areas where elk likely had well-defined and rapid increases in risk (<2,000 meters across). For example, the elk predation risk from wolves likely decreased farther from wolf-used trails in the Jasper-Willow Creek area, or the predation risk from humans decreased when entering national or provincial parks in the Bow watershed from hunted, multiple use lands. Along each transect, we located three risk level zones (high, moderate, and low risk of predation or hunting) to approximate Point A, the 30% twigs browsed isoline, and Point C respectively in figure 1. At five sample points in each zone, we counted pellet groups on a 2 x 50 m plot in the interior of an aspen stand paired to a stand edge plot in grasslands 10 to 30 m away. Where possible, aspen interior plots were established in thickets, defined as a dense stand (<1 meter spacing, >50 stems/100 m^2) of stems predominantly 2 to 6 meters in height. Where no thickets were found (low risk-high elk density areas), we paired edge plots to plots in the interior of aspen stands with the highest stem densities in the area. The moderate risk zone on each transect was recognized as the zone where saplings were relatively dense in and near aspen stands but rare in adjacent grasslands. Predictions of elk use of aspen patches versus adjacent grassland patches at three risk levels (table 3) were tested with a one-way analysis of variance of the ratio of paired values (aspen stand interior/edge of stand) of elk pellet group counts.

Elk Browsing Effects on Aspen

We estimated elk-aspen browsing levels on aspen at five points (10 m spacing) within each of the five 2 x 50 m paired plots at the low, moderate, and high risk points along each risk transect (see above). At each point, the nearest two aspen stems in each of three height classes (suckers [0 to 1 m], tall suckers [1 to 2 m], and saplings [2 to 6 m]) were tallied by live or dead condition and four browsing classes: <20% twigs browsed and/or stem debarked (BC1); 20 to 50% twigs browsed and/or stem debarked (BC2); 50 to 80% twigs browsed and/or stem debarked (BC3); and >80% twigs browsed and/or stem debarked. For analysis, an overall browsing index was calculated for saplings from the midpoint of each browse class, weighted by the number of stems in each class (BC 1 to BC4), and divided by the total number of stems (n), with the equation:

$$B = (0.1{*}BC1 + 0.35{*}BC2 + .65{*}BC3 + 0.9{*}BC4)/n$$

Predictions (table 2) of elk browsing intensity of aspen stems inside patches versus stems adjacent to grassland patches at three risk levels were tested with a one-way analysis of variance of the ratio of paired values (interior of aspen stand/edge of stand) of browse index values.

Few aspen thickets of stems 2 to 6 m in height occurred at the high elk density and low predation/hunting risk end of transects. To evaluate over-winter elk herbivory effects on sapling stands under these conditions, we constructed five artificial sapling thickets in the Banff-Bow Valley area (table 3). Methods followed Lundberg and Dannell (1990) and Edenius (1991). Unbrowsed aspen stems were cut during winter dormancy in December and early January from the nearby fenced highway wildlife exclosure. Each artificial thicket consisted of 36 stems (2 to 5 m in height) set 20 cm into frozen ground to form a thicket 4 x 4 meters (approximately 0.75 m spacing between stems). Ten stems were placed farther out, spaced 5 m apart, in the grassland area around the thicket. Thickets were built around one to three mature, single aspen stems (>5 m height). We measured the browsing condition class (see above) for each stem every 8 to 12 days after construction (early January 1999) until spring (late March). For analysis of browsing effects, the browsing index (see above) was calculated for each sample date for stems grouped as open (in the meadow), edge (on edge of thicket), interior (0.5 to 1 m inside the thicket), and core (center of thicket).

Results

Wolf scat abundance on main and side trails was different between the Banff-Bow and the Jasper-Willow Creek areas (table 4). Fencing prevents wolves from using the Trans Canada Highway in the Bow-Banff area, and wolf use, as indexed by scat counts, was relatively low along side trails within 1.5 km of the fenced highway. For the Jasper area, wolf scats were abundant on the main valley bottom trail and less common on side trails.

Factorial analysis results of elk pellet counts (table 5, figure 4) showed significant main effects of landscape area (Banff or Jasper), distance from trail or road, and patch type. Banff had higher pellet group counts than Jasper. For both areas, the pattern of elk pellet counts was grass > aspen > conifer. The interaction effect between landscape area and distance from trail or road was significant, demonstrating an opposite pattern of elk use in Banff and Jasper corridors near roads and trails. In Banff, elk use was highest near the highway, with consistently less elk use in all patch types with increasing distance classes. In Jasper, elk use was lowest near the trail but was more variable with distance from the trail (table 6). Contrary to predictions, there was no significant interaction between landscape, distance from trail or road, and patch type. The relative number of pellet groups within grass, aspen, and conifer patches was fairly consistent within distance and landscape area (figure 4).

Elk pellet group counts and browsing index values for paired aspen stand interior and edge plots varied significantly between plots that had different predation and hunting risk (figure 5). There were few elk pellets in both edge

Table 4—Trail and highway distances sampled and mean spring (May, June) wolf scat counts by cover type on trails for the Banff townsite area, Banff National Park, and Willow Creek area, Jasper National Park.

Type	Attribute patch type	Jasper-Willow Creek Grass	Jasper-Willow Creek Aspen	Jasper-Willow Creek Conifer	Banff-Bow Valley Grass	Banff-Bow Valley Aspen	Banff-Bow Valley Conifer
Main trail or highway	Distance (km)	9.5	0.6	12.5			
	Scat count	46	1	62		Fenced	
	Scats/km	4.8	1.6	5.0			
Side trail	Distance (km)	1.7	.4	2.3	7.9	1.2	21.2
	Scat count	8	0	1	5	0	13
	Scats/km	4.7	0	.4	0.63	0.0	0.61

Table 5—Results of the analysis of variance of the effects of landscape area (Banff-Bow Valley, Jasper-Willow Creek), distance from road or trail (near, moderate, and far), and patch type (grass, aspen, and conifer), on the square-root transformation of elk pellet group counts (mulitiple R = 0.745, multiple R^2 = 0.555).

Source of variation	SS	Df	MS	*F*-ratio	*P*
Landscape	390.66	1	390.66	387.81	0.000
Distance from road/trail	50.63	2	25.32	25.13	0.000
Patch type	202.86	2	101.43	100.69	0.000
Landscape x Distance	68.34	2	34.17	33.92	0.000
Landscape x Patch	6.81	2	1.70	1.69	0.151
Distance x Patch	53.48	4	26.74	26.55	0.000
Landscape x Distance x Patch	5.42	4	1.36	1.35	0.252
Transect (area)	95.20	8	11.90	11.81	0.000
Error	427.11	424	1.01		

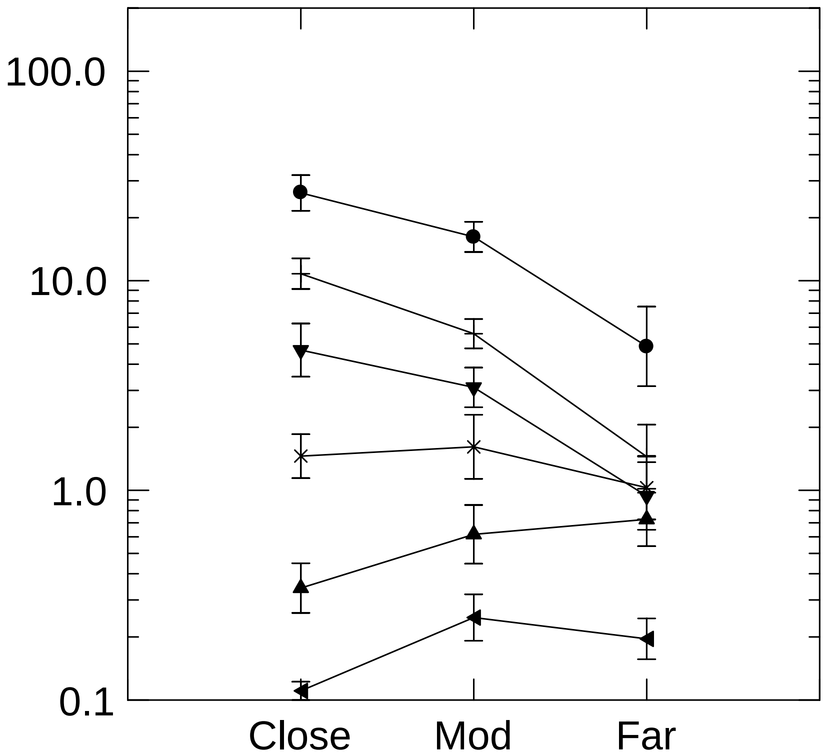

Figure 4—Geometric means ± SEM of elk pellet group counts for grass (G), aspen (A), and conifer (C) cover types at 3 distances from trails or roads in the Banff (B) and Jasper (J) study areas. The 1 pellet group/100 m² threshold line indicates the level above which aspen saplings are rare (C. White, personal observation). For each sample, n = 25.

Table 6—Mean pellet group counts/100 m² with standard error on mean for cover types within study areas. Column means with different superscript letters within areas and row means with different superscript numbers are significantly different (see text) at p<0.05 (Bonferroni test on square root of elk pellet counts). Sample sizes are n = 25 for plots grouped by landscape, distance, and patch type; n = 75 for plots grouped by patch types; n = 225 for each landscape, all distances and patches; n = 150 for plots grouped by cover for all distances; and n = 450 for all plots.

	Distance from	Patch type			For all	For all
Landscape	trail or road	Grass	Aspen	Conifer	patches	distances
Banff-Bow Valley	Close	38.6 ± 6.3	14.2 ± .0	7.9 ± 1.4	20.3 ± 2.8[a]	12.7 ± 1.2
	Moderate	19.6 ± 3.0	7.5 ± 1.0	4.7 ± 1.0	11.2 ± 1.5[b]	
	Far	13.9 ± 2.8	3.5 ± 0.7	2.7 ± 0.7	6.7 ± 1.1[c]	
Jasper-Willow Creek	Close	2.2 ± 0.4	0.6 ± 0.2	0.0 ± 0.0	1.0 ± 0.2[d]	1.4 ± 0.1
	Moderate	3.9 ± 0.7	1.4 ± 0.3	0.4 ± 0.1	2.0 ± 0.3[e]	
	Far	2.4 ± 0.5	1.3 ± 0.2	0.3 ± 0.1	1.3 ± 0.2[d]	
For both landscapes	All distances	13.7 ± 1.7[1]	4.7 ± 0.6[2]	2.7 ± 0.4[3]	—	7.0±0.6

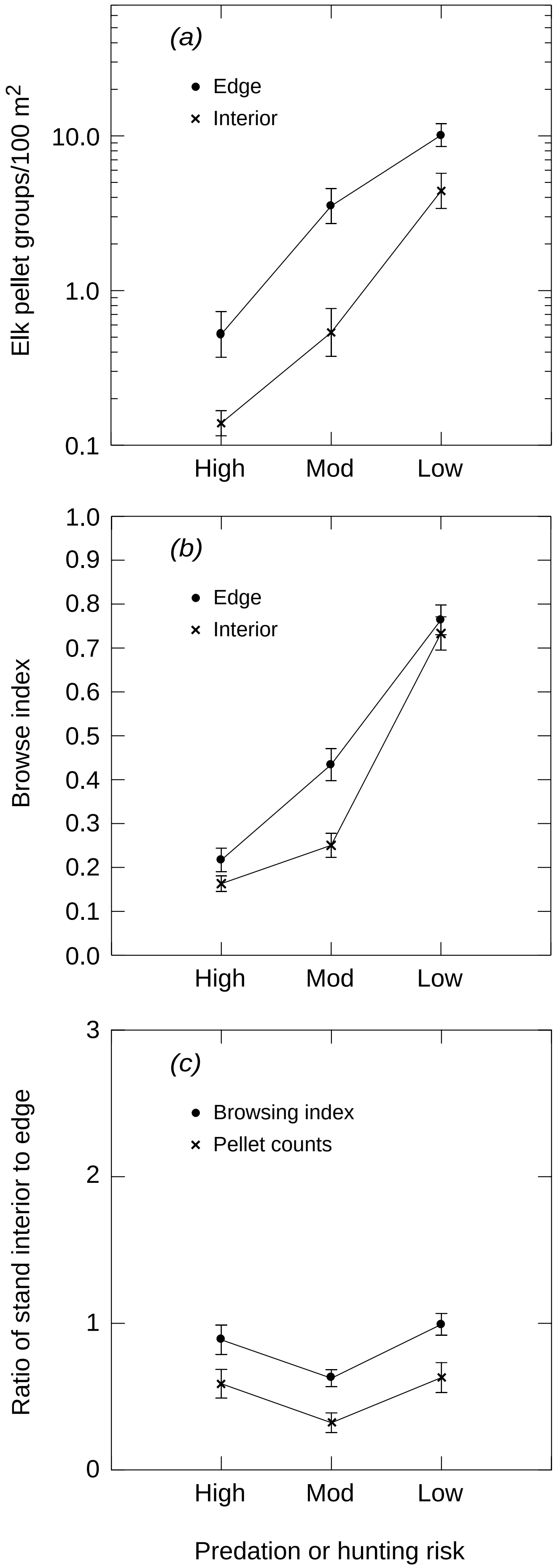

Figure 5—Means ± SEM of pellet group counts (*a*) and browsing index values (*b*) for paired plots on the edge and in the interior of aspen stands on transects from high to low predation or hunting risk to elk, and the ratio of interior to edge pellet count and browse index values (*c*). For each sample, $n = 25$.

and aspen interior plots in high-risk areas. Pellet numbers increased more rapidly in edge plots than aspen interior plots as risk decreased (figure 5a). Areas at moderate risk had a statistically significantly lower (p = 0.03, Bonferroni adjusted) ratio of interior to edge pellet group counts (figure 4c) than did low risk areas. Aspen sapling browsing index values had a corresponding pattern (figure 5b). The stand interior to edge ratio of browsing (figure 5c) was significantly lower in moderate than in high risk areas (p = 0.04, Bonferroni adjusted) and low risk areas (p = 0.001, Bonferroni adjusted). These use patterns corresponded with changing aspen stand structure. Aspen stands in moderate and high risk areas were dense and multi-aged (figure 6a). However, in lower risk areas where pellet counts were >1 group/100 m^2, stands had low sapling densities and were much more open (figure 6b).

Over-winter (approximately January 10 to March 20) browsing by elk was intense on the model aspen stands constructed in the Banff-Bow area. Browsing index values decreased for stem placements in the following order: isolated stems in open areas, stems on the edge of 4 x 4 m thickets, stems 1 m in from thicket edge, and stems in center of thickets (figure 7). By the end of winter, the mean browsing index was greater than 0.7 for all stem placements.

Discussion

Effects of Patch Type and Travel Corridors Used by Predators and Humans

General elk use by patch type (grass > aspen > conifer), as indexed by pellet group counts (figure 4, table 6), was consistent for the Jasper and Banff areas. High elk use of grass and short shrub habitat patches has been reported for numerous Rocky Mountain areas including northern British Columbia (Peck and Peek 1991), Alberta National Parks (Cowan 1947; Flook 1964), Montana (Jenkins and Wright 1988), Yellowstone National Park (Houston 1982; Coughenour and Singer 1996), and lodgepole pine and meadow areas in Utah (Collins and Urness 1979). Pellet group counts were comparable to earlier research (1975 to 1980) in the montane ecoregion in Banff and Jasper National Parks where means of 10 to 15 groups/100 m^2 for grassland types and 2 to 4 groups/100 m^2 for forest types were reported (Holroyd and Van Tighem (1983: 412).

The different patterns of elk pellet groups near valley bottom trails in a wilderness area of Jasper National Park in contrast to near a busy four-lane highway in Banff National Park (figure 4) were in accordance with predictions (table 1). In the Banff area, there was consistently fewer elk pellet groups as the distance from the highway increased (table 6). This may be the result of predator avoidance (Dekker et al. 1995). In Banff, wolves cannot use the highway as a valley-bottom travel vector due to highway fencing (table 4), and only infrequently use areas near the fence due to high traffic volume. Paquet et al. (1996) found from tracking and radio telemetry studies that wolves avoided areas within 500 m of the highway in Banff. Dekker et al. (1995) described a similar pattern of relatively low wolf use and high elk use near the main highway in the Athabasca Valley in Jasper National Park. However, in the Athabasca Valley, elk could also be attracted to the highway right-of-ways because of tree clearing and agricultural grass cover (Holroyd and Van Tighem 1983). In the Banff area, highway fencing blocks elk use on most of the right-of-way area (Woods 1990), thus reducing the effect of this confounding factor.

Figure 6—Dense stand of aspen saplings near a trail heavily used by wolves at Willow Creek in Jasper National Park, Alberta (a, upper photo), and heavily browsed, low stem-density stand approximately 500 m from the trail (b, lower photo).

In the Jasper-Willow Creek area, the valley bottom trail was a main winter travel vector for wolves (table 4). This corroborated the findings of several other studies of wolf movements in undeveloped areas of the Rocky Mountains (Carbyn 1974; Paquet et al. 1996; Kunkel 1997). In winter at Willow Creek, wolves maintain runways through snow along trails by repeatedly using the same route (Carbyn 1974). In addition, Jasper National Park wardens make infrequent winter patrols on the main trail by snow machine (G. Antoniuk, personal communication). Trails where the snow is packed, but are only lightly

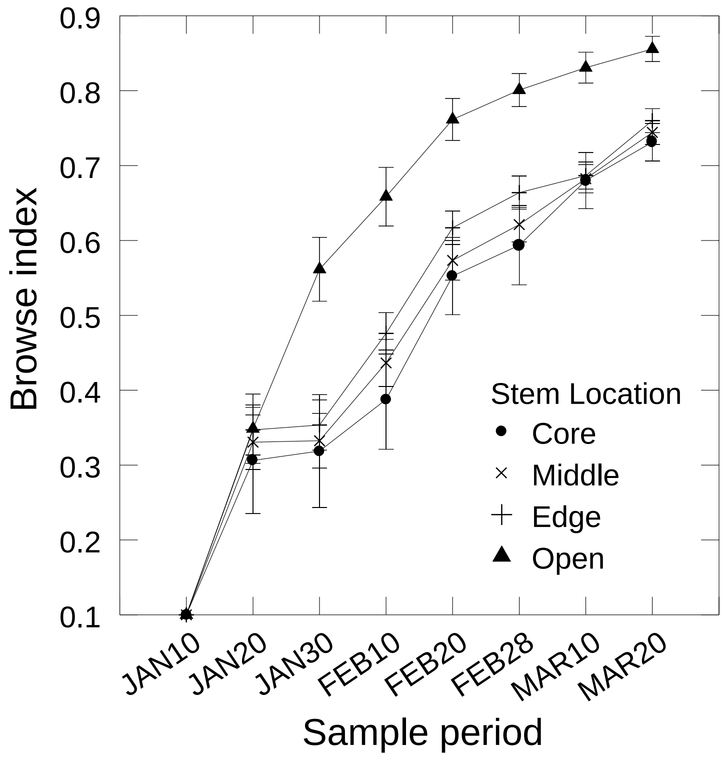

Figure 7—Mean ± SEM of browsing index values of aspen stems in and near model thickets. See text for location of stems. Sample sizes are open stems (*n* = 50), edge stems (*n* = 100), interior stems (*n* = 60), and core stems (*n* = 20).

used by people, are often preferred winter travel routes for wolves (Paquet et al. 1996). There was significantly less elk use within 100 m of the Jasper trail, but elk use was more variable with distance than in Banff (figure 4, table 6). In contrast to Banff where wolves predictably avoid areas close to the highway (Paquet et al. 1996), Jasper wolves may use main trails heavily but they still utilize side trails and areas away from trails (table 4). Further, predators such as cougar, black bear (*Ursus americanus*), and grizzly bear (*Ursus arctos*) are likely more common at all distances from trails in the remote Jasper area compared to near the highway in the busy Banff area (Banff Bow Valley Study 1996).

Contrary to predictions for an interaction effect on elk habitat use that included distance from trail or road (figure 4, table 2), there appeared to be similar relative elk use patterns for patch types (e.g., grass >> aspen > conifer for Banff, grass > aspen >> conifer for Jasper) for all distances within landscapes. Possibly, elk use of adjacent patches types as sampled with our methods was not independent. Elk often forage in grass patches, but may seek hiding cover in adjacent conifer patches when resting (Lyon 1979; Lyon and Ward 1982; Thomas et al. 1988). However, the low number of pellet groups in the aspen and conifer types closer to trails in the Jasper-Willow Creek area (table 6) suggested that elk avoided forest cover here when foraging or traveling.

The overall patterns of elk use with landscape, distance from trail or road, and patch type had important biological significance for aspen regeneration. In Jasper, aspen saplings within aspen and conifer patches near the trail were often unbrowsed (figure 6a). However, in all patch types at all distances from the road in Banff, Jasper aspen patches >500 m from the trail, and all Jasper grasslands, pellet group counts exceeded the threshold of ≈1 group/100 m^2 (C. White, personal observation) where aspen saplings are completely browsed off (figures 4, 6b).

Effects of Aspen Stand Structure and Predation Risk

Elk pellet group and browsing index values for paired aspen interior and grassland edge across predation and hunting risk gradients (figure 5) followed the predictions from risk-sensitive foraging (table 2). These results support the hypothesis that the Type 2 functional response observed for aspen sapling-elk interaction (figure 2) is at least partially caused by relatively less time spent by elk in dense-stemmed aspen patches. Along risk gradients (figure 5), this interaction was most clearly manifested at intermediate risk levels. At high risk, elk densities were low and elk browsing was low in both the edge of and inside adjacent aspen thickets (figure 6a). At low risk, elk were at higher densities and over time killed aspen saplings (figure 6b). The remaining open-grown stands were again more equitably used by elk in comparison to adjacent grasslands (figure 5c). At intermediate risk, elk densities were moderate in grasslands, but they most clearly avoided using aspen thickets. Further evidence of this fine-scale elk-foraging pattern was provided by browsing over time in the model thickets built in the Banff's Bow Valley. Elk browsed sapling stems in open grasslands near stand edges preferentially (figure 7). However, in this high elk density situation, even stems at the core of aspen thickets were heavily browsed within 90 days of stand construction. Shepperd and Fairweather (1994) observed comparably high elk browsing rates when fences protecting sapling stands in Arizona were removed.

The relatively low rates of browsing of aspen suckers and saplings in multi-aged, high stem density stands compared to more open aspen stands has been recognized by previous researchers (DeByle 1985a,b). The low elk use of dense aspen stands we observed could be the result of an interrelated suite of factors. Dense stands may have better cover for stalking predators such as cougars (Kunkel et al. 1999), increased snow depths (Telfer 1978), and decreased forage availability (Bailey and Wroe 1974). In contrast, adjacent open grassland areas provide elk with ease of escape from predators (Geist 1982), and when elk numbers are low, open grasslands provide a high availability of palatable grasses (Willoughby et al. 1997).

Plant structural characteristics such as thorns, spine, tough leaves, and prickles may reduce herbivore use (Harper 1977; Cooper and Owen-Smith 1986; Pollard 1992). But intuitively, increasing density of highly palatable forage such as aspen saplings would result in higher herbivore use of patches, not lower, if no other factors were operative. However, aspen communities exist in montane landscapes that historically included not just plants and herbivores, but also predators—humans, wolves, cougars, and black and grizzly bears (Mattson 1997; Kay 1998; White et al. 1998a; Kunkel et al. 1999). In three-level trophic systems, the interaction between vegetation structure, predator hunting behavior, and herbivore response to predation risk is likely profound, variable, and complex (Lima and Dill 1990; Hunter and Price 1992; Lima 1998; Kie 1999). Results of the present study suggest the hypothesis that aspen's dense-stemmed thicket trait confers increased fitness to aspen clones in predator-rich environments but could be detrimental in herbivore-rich situations. This requires further investigation.

Integration of Risk-Sensitive Foraging Patterns and Aspen Stand Structure

The three spatial scales of elk density and risk-sensitive foraging patterns (figure 3) evaluated here (regional, near trails and roads, and habitat patch level) appear to be associated with major structural differences in aspen stands. At the regional level in high-predation risk areas, such as Jasper's Willow Creek where elk densities were low (<1 pellet group/100 m^2; figure 4), aspen were often multi-aged and dense (figure 6a). In low-predation and hunting-risk areas, such as in Banff, elk densities were usually high (>3 to 5 pellet groups/100 m^2; figure 4). Under these conditions, all aspen stands were heavily browsed, and dense multi-aged stands did not occur.

At intermediate spatial scales, human and predator travel routes had completely different effects under different risk situations. In high-predation risk ecosystems with low human use, valley-bottom trails were frequented by wolves (table 4). Elk were not attracted to these trails, and may even have avoided some areas near them (figure 4). As a result, in the Jasper Willow-Creek area, aspen stands were multi-aged and most dense near the main trail, and more heavily browsed at increased distances from the trail (figure 6). In low-predation risk areas (e.g., near busy national park roadways) the opposite effect occurred. Elk may be attracted to valley bottom travel routes and facilities heavily used by humans but avoided by wolves (Paquet et al. 1996). This resulted in very high elk densities in aspen stands (e.g., >10 pellet group/100 m^2) such as observed in this study for the Banff's Bow Valley (figure 4). This "reversed" pattern of elk use in modern park landscapes makes herbivory impacts acute for aspen stands in valley-bottom areas once heavily used, but now avoided, by predators (Ripple and Larsen 2000).

At the finest scale of the habitat patch, structural conditions of aspen (low density stands versus dense, multi-aged stands) further affected elk foraging behavior. In a high-predator risk region, particularly near routes frequented by predators, aspen stands had high stem densities with low browsing rates (figures 5b, 6a). In contrast, a positive feedback mechanism occurred when elk densities were high—browsing reduced stem density, which increased elk habitat use and browsing rates. Most aspen stands in low-predation risk and high elk density areas in the Rocky Mountains are currently in this condition (Kay 1997a). From 1940 to 1970, several national parks including Jasper, Banff, Yellowstone, and Rocky Mountain culled elk but achieved no significant response from aspen (White et al. 1998a), even when elk populations were reduced to levels where aspen regeneration had previously occurred (Houston 1982; Huff and Varley 1999). This led to alternative hypotheses that fire suppression or climate change were important causes of aspen decline (Houston 1982; Romme et al. 1995). However, results of our study suggest that aspen regeneration would not be expected at the same elk densities at which it initially declined due to different elk behavioral patterns in remnant open stands (figure 2). Only a major decrease in elk density would re-create the dense multi-aged stands that are more resistant to herbivory.

Historically, spatial factors that affected predation on herbivores—such as predator travel routes (Carbyn 1974), wolf pack buffer zones (Mech 1977), and denning locations (Dekker et al. 1995) or First Nation intertribal warfare areas (Kay 1994; Martin and Szuter 1999)—likely shifted with time. The resulting spatially dynamic, risk-sensitive foraging patterns of elk would often provide conditions favorable for creating dense aspen stands that would be resistant to periodic higher densities of elk if predation risk declined. In contrast, many current risk zones (e.g., park boundaries) are spatially fixed and may result in long-term high elk density in some areas (White et al. 1998a).

The landscape analysis, or "natural experiment" technique, used here to evaluate hypotheses for risk-sensitive foraging by elk on aspen did not control for the relative effects of predation risk versus elk competition for food. For example, in all analyses, areas of higher risk had lower densities of elk, as indexed by pellet groups (figures 4, 5b; table 6). Relatively low browsing rates on aspen in these areas could be more related to the higher availability of preferred foods (e.g., some grass species) in low elk density areas than risk-driven avoidance of aspen stands. However, reductions in elk density at local or regional levels, through behavioral or demographic effects, may be a relatively consistent result of increased carnivore predation or human hunting rates (Lyon and Ward 1982; Dekker et al. 1995; Paquet et al. 1996; Kunkel and Pletscher 1999).

Conclusion

Patterns of elk herbivory on aspen result from multi-scale factors that include not just general elk density, but varying risk-sensitive foraging patterns resulting from predator habitat use (Ripple and Larsen 2000) and aspen stem-density conditions. In national parks of the Canadian Rockies that are heavily used by people, the current pattern is one of high-density elk populations attracted to valley bottoms and intense elk foraging on low stem-density aspen stands. This is the opposite of historical conditions throughout the Rockies and of the current situation in more remote areas, where elk have lower densities and are not attracted to valley bottom travel routes that are heavily used by wolves or human hunters. Low herbivory results in dense, multi-aged aspen stands that are resistant to periodically higher browsing rates by fluctuating populations of elk. This condition is likely similar to the long-term spatially dynamic conditions that maintained aspen in valley-bottom areas.

Elk-aspen foraging patterns result from complex interactions between predators, herbivores, and vegetation. As predicted by Hunter and Price (1992), these interactions are highly influenced by heterogeneity in more natural systems where predators still occur. Neither "top-down" nor "bottom-up" influences necessarily prevail. However, reductions in elk density at local or regional levels, through behavioral or demographic effects, may be a consistent result of maintaining the historical range of variability of carnivore predation or human hunting rates. Therefore, it may be difficult to isolate the effects of predation from reduced elk competition for food in future research on aspen herbivory. Results of this study suggest the hypothesis that aspen's dense-stemmed thicket trait confers increased fitness to aspen clones when interactions occur between the behavior of predators and herbivores and the density of vegetation.

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