Do high-density patches of coarse wood and regenerating saplings create browsing refugia for aspen (*Populus tremuloides* Michx.) in Yellowstone National Park (USA)?

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Abstract

Following the extensive 1988 fires in Yellowstone, a mosaic of high-density patches of fallen logs and regenerating lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex Wats.) saplings developed in the landscape. Such patches could potentially provide browsing refugia for post-fire aspen (*Populus tremuloides* Michx.) seedlings. We asked two primary research questions: (1) Do elk (*Cervus elaphus* L.) reduce their use of high-density patches of coarse-wood and pine saplings? and (2) Are the abundance, height, and probability of presence of aspen positively related to the density of coarse wood or pine saplings? We visited 65 sites distributed across density gradients of downed wood and regenerating saplings. At each site, aspen seedlings were counted along five 50 m × 2 m belt transects. The height, basal diameter and presence of browse damage were recorded for each individual. Fallen logs and elk fecal pellet groups were counted along the same transects. Aspen seedlings were heavily browsed throughout the study area and were less likely to be found near high-elevation meadows. Variation in elk pellet densities was not explained by the density of logs at the scale of the transect or the site. The height of aspen seedlings was not related to density of logs, pine saplings or elk fecal pellet groups. However, taller aspen were found at higher elevations and with more open meadow in the landscape. This suggests that later snowmelt and alternative forage may reduce browsing pressure on aspen. Given that some of the sites had densities of pine saplings in excess of 60,000 stems ha^{-1} and densities of downed logs greater than 2000 logs ha^{-1}, these results suggest that fire-induced coarse wood and pine saplings will not create broad-scale browsing refugia for aspen in the landscape of the Yellowstone plateau.

Keywords: Elk; Wapiti; Lodgepole pine; Quaking aspen; Plant–herbivore interactions

1. Introduction

An important challenge facing contemporary ecologists is understanding the ways that organisms create and respond to resource heterogeneity (Levin, 1992; Turner, 2005). It is especially important to develop this understanding in systems where large, mobile herbivores have the potential to interact with ecosystem processes at broad spatial scales. Such herbivores discriminate among spatially variable food resources, and may in turn alter the structure of plant communities and the rates of ecosystem processes (Pastor et al., 1993, 1998; Merrill et al.,

1994; Waller and Alverson, 1997; Frank and Groffman, 1998a,b; Ritchie et al., 1998; Rooney et al., 2002; Collins and Smith, 2006; Anderson et al., 2007). Improving our knowledge of the responses of large herbivores to spatial heterogeneity can contribute to understanding these and other ecological processes.

The link between large herbivores and plant communities is of current interest in the Rocky Mountain region of the United States. Over the last several decades, quaking aspen (*Populus tremuloides* Michx.) stands have been reported to be declining in many areas of the intermountain west (Kay, 1997; Shepperd et al., 2001). However, recent landscape-scale research suggests that this decline is not ubiquitous across the region (Suzuki et al., 1999; Barnett and Stohlgren, 2001; Kaye et al., 2003). Much of the blame for the decline, when present, is attributed to fire suppression and heavy browsing by wild ungulates, especially elk (*Cervus elaphus* L.) (Baker et al., 1997; Shepperd et al., 2001).

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Concern over the fate of aspen is especially acute in Yellowstone National Park (YNP), where the elk herd has been directly implicated in the local decline of aspen, at least in an area known as the Northern Range located in the northern portion of the park (Houston, 1982; National Research Council, 2002). Ripple and Larsen (2000) found that nearly 95% of the mature aspen stems in the Northern Range originated prior to 1920. Although the Northern Range serves as a wintering area for a large herd of elk, the apparent decline of aspen since the late 1800s may be the effect of a combination of factors including climatic variation, browsing and fire (Romme et al., 1995). Wintering elk densities at that time may have been as great or greater than the current density (Houston, 1982); however, trophic interactions may have produced behavioral responses by the elk that allowed for an aspen release prior to the predator eradication program of the early 1900s (Ripple and Larsen, 2000; Beschta, 2003, 2005; Ripple and Beschta, 2004a; Fortin et al., 2005).

Another factor that strongly influenced habitat use by elk and the extent of aspen regeneration in the park was the extensive fires of 1988. In the years following the fires, aspen seedlings were discovered in many areas of the burn representing one of the few contemporary examples of broad-scale sexual reproduction of aspen in the Rocky Mountains (Baker, 1925; McDonough, 1985; Kay, 1993; Romme et al., 1997; Turner et al., 2003). Patterns of elk habitat use were influenced for 3–5 years by the abundant and nutritious forage stimulated by the fires (Turner et al., 1994b; Pearson et al., 1995; Boyce and Merrill, 1996; Singer and Harter, 1996). However, elk may still be responding to other fire-induced patterns that are more persistent in the landscape.

In the 1990s, regenerating pine sapling densities in the 1988 burn extent ranged from zero to more than 500,000 saplings ha^{-1} (Turner et al., 1997, 1999, 2004; Kashian et al., 2004). As these saplings were growing, fire-killed trees fell to form an extremely heterogeneous distribution of coarse wood patches that ranged up to 2 m deep (Ripple and Larsen, 2001; Romme et al., 2005). We define a patch as a relatively homogeneous distribution of coarse wood with an extent of at least 0.5 ha. Densities of coarse wood and regenerating saplings will influence the ease with which elk can move through patches (Parker et al., 1984), a feature we refer to as "impedance". Because patches with higher impedance will have greater travel costs, foraging theory predicts that elk will tend to "over-match" resources (Kennedy and Gray, 1993). High-impedance patches with high food quality will therefore receive less foraging pressure than expected if herbivores followed an Ideal Free Distribution (Fretwell and Lucas, 1970). Such a reduction of foraging pressure in high-impedance patches may effectively create broad-scale refugia throughout the landscape for aspen and other preferred forage species.

Associational refugia (sensu Pfister and Hay, 1988) have been demonstrated to reduce herbivory in both aquatic (Kerr and Paul, 1995; Wahl and Hay, 1995) and terrestrial communities (Mulder and Ruess, 1998). While some associational refugia occur due to the density of unpalatable species (Atsatt and Odowd, 1976), physical refugia are common in

large herbivore systems (Borgmann et al., 1999; Garcia et al., 2000; Rousset and Lepart, 2000; Rebollo et al., 2005). For example, eastern hemlock (*Tsuga canadensis* [L.] Carr.) seedlings grow taller in high-impedance patches created by dense balsam fir (*Abies balsamea* [L.] Mill.) due to reduced herbivory by white-tailed deer (*Odocoileus virginianus* Zimmerman) (Borgmann et al., 1999). Likewise, non-living refugia such as rock outcrops, steep slopes, and log piles have been associated with higher floral species diversity and growth of aspen suckers compared to grazed areas outside the refugia (Rumble et al., 1996; see a review by Milchunas and Noy-Meir, 2002). In one study, log refugia were the only places where sexually reproducing individuals of some shrub species could be found (Schreiner et al., 1996). However, the efficacy of log refugia is not universal (Kupferschmid and Bugmann, 2005).

Artificial elk exclosures in YNP have produced inconclusive evidence regarding the effects of grazing and browsing on species diversity and aspen growth (Stohlgren et al., 1997; Romme et al., 2005), but some research suggests that aspen saplings growing through log piles are taller and less browsed than saplings elsewhere (Ripple and Larsen, 2001; Romme et al., 2005). However, in an earlier study only 2 years after the fire, Romme et al. (1995) observed that aspen shoots were evenly browsed in both burned and unburned aspen stands throughout the Northern Range. This contrast suggests that the gradually increasing coarse wood piles (and possibly dense lodgepole pine [*Pinus contorta* var. *latifolia* Englem. ex Wats.] regeneration) are providing important refugia for aspen and other species in the Yellowstone landscape. It is unclear if the broad-scale accumulation of coarse wood will affect elk habitat use or browsing intensity on aspen.

We were interested in determining if disturbance-induced impedance assessed at the patch-scale affected the habitat use of elk or the growth of aspen saplings. To assess these effects we considered two research questions: (1) Do elk avoid high-impedance patches? and (2) Is there a relationship between impedance and the presence, abundance or height of aspen saplings? Although the process of browsing occurs at the micro-scale, we assumed that elk make foraging decisions in a hierarchical fashion (Senft et al., 1987) and will choose feeding areas (patches) based on patch-level characteristics. Because elk are social animals and are under moderate predation pressure from wolves (*Canis lupus* L.), they should prefer areas that provide some hiding cover but are easy to move through. Thus, we expected that moderately dense thickets of lodgepole pine saplings would be preferred, while areas of extremely dense thickets and coarse wood piles would be avoided. Likewise, we hypothesized that aspen seedlings would be more numerous and taller in areas with fewer elk and higher impedance.

2. Materials and methods

2.1. Study area

This study was conducted during the summers of 2003 and 2004 in Yellowstone National Park (YNP). The park encompasses ca. 9000 km^2 in the northwest corner of Wyoming

and adjacent parts of Montana and Idaho (USA). Elevations in the park range from 1500 to more than 3000 m, but much of the park is dominated by sub-alpine plateaus (Houston, 1982; Despain, 1990). The plateaus are primarily covered with lodgepole pine (*P. contorta* var. *latifolia*) forests of varying age, a large proportion of which are regenerating stands that originated after the 1988 fires (Despain, 1990; Turner et al., 1994a). Pine sapling densities range from 0 to more than 500,000 ha^{-1} in these 15-year-old stands (Turner et al., 2004). Aspen seedlings, which germinated patchily throughout much of the burn extent, have densities ranging from 0 to 46,000 ha^{-1} (Kay, 1993; Romme et al., 1997; Turner et al., 2003). Although these aspen are heavily browsed in the summer range, ungulate densities are low in this area and do not appear to be resource limited (National Research Council, 2002).

2.2. Data collection

Sixty-five 0.5 ha sites were stratified across a range of coarse-wood densities throughout the extent of the 1988 fires (Fig. 1). Fifty-five of these sites were selected from 113 sites at which coarse-wood densities were already measured (Heather Lyons and William Romme, unpublished data). The original 113 sites were randomly located within the 1988 burn extent, but were restricted between 0.5 and 1.5 km of a road and stratified such that all four cardinal aspects received an equal number of sites.
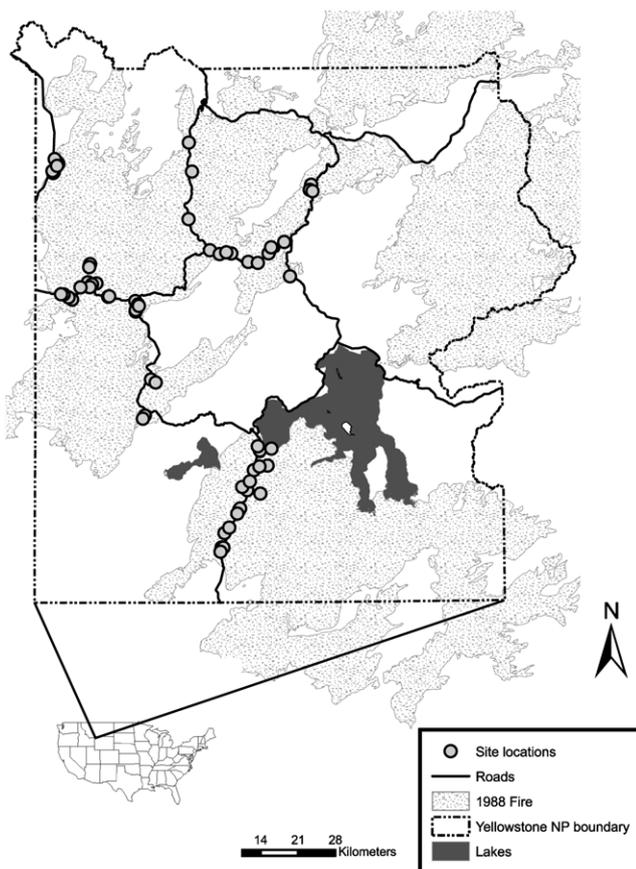

Fig. 1. A map of Yellowstone National Park with the 1988 burn extent and site locations (○) identified.

Because we expected that coarse wood would only have an influence at the higher end of the density spectrum, we chose all sites within the top quartile of coarse-wood density ($n = 29$) and randomly selected 26 of the remaining sites. The final 10 site locations were randomly located in regions within 4 km of a road known to have high densities of coarse wood (William Romme, personal communication). At these 10 locations, we applied the same methods used to calculate coarse-wood density at the other sites (methods described below). For all sites, we calculated landscape covariates other studies have shown to affect the habitat use of elk. The landscape cover-type composition (calculated for a circular 700 m buffer around each site's center point), relative wolf density (a kernel-density estimate based on the summer locations of each pack, see Forester et al. (2007) for more details), and distance to large open areas (contiguous grassland areas ≥1 ha) were determined for the center point of each sapling site (Table 1). The choice of buffer size was based on doubling the median 5-h movement distance of elk in YNP (Forester et al., 2007). To calculate the covariates, we used a Geographic Information System (GIS, ESRI ArcGIS 9.0) and numerous spatial data sets either provided by the Yellowstone Center for Resources (YCR) or created for this project (Forester, 2005). Sites were visited only once, so to avoid a temporal bias, sites were visited in random order between 1 July and 24 August 2003 ($n = 62$). The final three sites were visited on 14 and 15 July 2004.

2.2.1. Pellet density

At each site, five parallel, 50 m × 2 m belt transects were established 25 m apart on a bearing perpendicular to the slope. Fecal pellet groups were defined as a cluster of pellets ≥1 m from any other cluster, or of distinctly different size or age. Pellet groups within each belt transect were counted after being identified to species based on pellet morphology (Halfpenny and Biesiot, 1986). Although it can be difficult to make a distinction between small elk pellets and large mule deer (*Odocoileus hemionus*) pellets, the latter species is much less abundant in our study area, so overlap was assumed to be small (Houston, 1982). Each pellet group was assigned an age class based on a qualitative assessment of its state of decomposition: (1) fresh or dry pellets with a glossy surface and no sign of weathering; (2) surface mostly glossy with some cracks; (3) surface broken and extensively weathered.

To assess qualitatively the effect of within-season weathering on pellets, a set of four fresh pellet groups was placed in an exposed area, with ground-cover typical of regenerating coniferous stands, and observed weekly from early July to late August of 2002. Longer-term weathering was assessed by distributing 12 fresh pellet groups among three different regenerating coniferous sites (>10 km apart) in August 2003. Pellets were digitally photographed at time of placement and again 1 year later (the four original groups were re-photographed 2 years later).

2.2.2. Coarse-wood density

To estimate the transect-level abundance of wood, all logs or branches with diameter ≥4 cm at the centerline of each pellet

Table 1
A list of covariates considered in the analyses

Class	Covariate	Abbreviation	Units	Range	Source
PELLET DENSITY	Pellet density by transect	PELTRANS	Pellets ha^{-1}	0–1200	Field samples
	Pellet density by site	PELLETDENS	Pellets ha^{-1}	0–720	Field samples
WOLF	Relative wolf density	WOLF	Unitless	0–95	YNP YCR
FORAGE	Herbaceous biomass	HERB	g m^{-2}	6.9–193.1	Field samples
TOPOGRAPHY	Elevation	ELEVATION	m	2043–2681	USGS DEM
	Slope	SLOPE	Degrees	0–31.5	USGS DEM
COVER	Distance to open area ($\geq$1 ha)	DOPEN	m	0–1344	Landcover map
	Open area in 700 m radius	OPEN	Proportion	0–0.60	Landcover map
IMPEDANCE	#Logs >4 cm diameter per transect	LOGTRANS	Logs transect^{-1}	6–146	Field samples
	Site density of logs (DBH $\geq$5 cm)	LOGSHA	Logs ha^{-1}	100–2134	Field samples
	Mean DBH of logs by site	LOGDBH	cm	11.1–31.9	Field samples
	Lodgepole pine saplings site^{-1}	SAPDENS	Saplings ha^{-1}	100–66,000	Field samples
	Qualitative sapling impedance	SAPLING	Low, med, high	NA	Field samples

transect were counted. The site-level abundance of coarse wood was quantified by more intensive sampling of wider transects centered on the first, third and fifth transects. The diameter at breast height (measured at 1.4 m from the base of the log; DBH) was measured for all logs (DBH $\geq$ 5 cm) that had a base located within 2 m of the three transect centerlines (i.e. within three, 200 m^2 transects). The density (logs ha^{-1}) and size distribution (mean and standard deviation of DBH) were calculated for the downed logs.

2.2.3. Forage biomass and sapling density

Percent cover of each plant species was visually estimated within ten 0.25 m^2 quadrats spaced at 5 m intervals along, and 2 m perpendicular to the centerline of the middle transect (transect 3). These percent-cover values were converted to biomass (g m^{-2}) based on allometrics described by Turner et al. (2004). At 32 sites, all coniferous saplings were counted within the middle 50 m × 2 m transect, this count was used to estimate sapling density for those sites; however, due to heterogeneous distributions of pine saplings (Turner et al., 2004), this density serves mainly as a relative measure of sapling density. At all sites, prior to collecting data, a three-level qualitative estimate of coniferous sapling impedance (low: visibility and movement not impeded, medium: visibility impeded without affecting movement, and high: visibility and movement impeded) was recorded. All aspen saplings and seedlings encountered along the five pellet-count transects were measured (basal diameter and height), and inspected for the presence of ungulate browse damage.

2.3. Statistical analysis

We used generalized linear mixed-effects models (GLMM) with a logit link to determine how transect-level and site-level covariates affected the presence or absence of elk pellets (pellets of ages 1 and 2 were combined for these analyses) and aspen seedlings. Transect-level and site-level analyses tested for effects at the sub-hectare and landscape scales, respectively. If there was no effect of transect, generalized linear models (GLMs) were

applied to the site-level data. Linear regression (generalized least squares, GLS) was used to determine what site-level factors affected the density of elk pellets at a site. For all sites at which aspen seedlings were present, the density and maximum height of seedlings were regressed against site-level variables. Covariates for all models were selected to represent impedance (coarse-wood density and pine sapling impedance), forage availability, relative wolf density and landscape composition (Table 1). A quadratic term for coarse-wood density was used to test our hypothesis of an intermediate impedance preference by elk. Distance to road was included in all of the global models for pellet presence and density to test for road-induced bias. Because of our two-stage sample design, coarse-wood density was included in all models, regardless of significance.

In all linear regressions, the dependent variables were square-root transformed to remove heteroscedasticity. Independent variables were checked for collinearity prior to analysis and all final models were chosen using AIC-based stepwise selection. The covariance structure of all linear models included an exponential variogram to account for spatial autocorrelation among sites. Following model selection, the mean model was re-fit under three alternate error structures (exponential, spherical or no variogram). The final error structure was chosen based on the results of a likelihood ratio test. All statistical analyses were carried out in R (R Development Core Team, 2005); additional packages used were nlme and lme4 (Pinheiro and Bates, 2000).

3. Results

3.1. Data summary

3.1.1. Pellet density

New pellet groups (ages 1 and 2) were rare in the burned landscape, with zero or one pellet group recorded on most transects (n = 126 and 76 transects, respectively). However, these pellet groups tended to be patchily distributed within sites, resulting in 37 sites with more than 5 pellet groups. Our observations of pellet group weathering showed that

decomposition of pellets in these stands is very slow (the original four pellet groups were still intact after 2 years). By observing the change in appearance of pellet groups through time (based on field observations and a visual comparison of digital photographs), we determined that our age classes correspond with <1 month (1), 1–3 months (2), and ≥1 year (3). We also found that observation of pellets 1 year or older can be impeded by graminoid vegetation that cures and then packs on top of the pellets during the winter. For this reason, we limited all analyses to pellets we were confident were deposited more recently than a year. Because elk do not typically winter in these areas, all pellets of age classes 1 and 2 were assumed to have been deposited during the spring and summer months of the same year.

3.1.2. Coarse-wood density

The sites we visited represented a wide range of coarse-wood densities (100–2134 logs ha^{-1}, mean = 744.15, S.D. = 379.45). As expected, the mean log DBH was negatively correlated with logs per hectare ($r = -0.72$, $p < 0.0001$). Likewise, the average number of logs and large branches intersecting each transect was positively correlated with logs per hectare ($r = 0.68$, $p < 0.0001$), and not highly variable within site (mean(CV) = 0.28, S.D.(CV) = 0.14). Large areas with extremely dense coarse wood (≥1000 logs ha^{-1}) are not common in the landscape; however, because 10 sites were specifically chosen from areas known to have dense wood, 13 (20%) of our sites fall within this category.

3.1.3. Forage biomass and sapling density

Herbaceous biomass was highly variable both within and among sites. Among sites, biomass ranged from 0 to 383.12 g m^{-2} (mean = 81.69 g m^{-2}, S.D. = 74.91). The within-site variation was also high, with an average coefficient of variation (CV) of 0.78 (S.D.(CV) = 0.41, range(CV) = 0.26–1.96). The density of lodgepole pine saplings was on average high (mean = 14,536 stems ha^{-1}) but spatially variable (S.D. = 20,405, CV = 1.40) and correlated to sapling impedance (Spearman's $\rho = 0.858$, permutation $p < 0.0001$). Aspen densities ranged from 0 to 3270 stems ha^{-1} and were present in 74 transects at 31 sites (mean site density when pre-
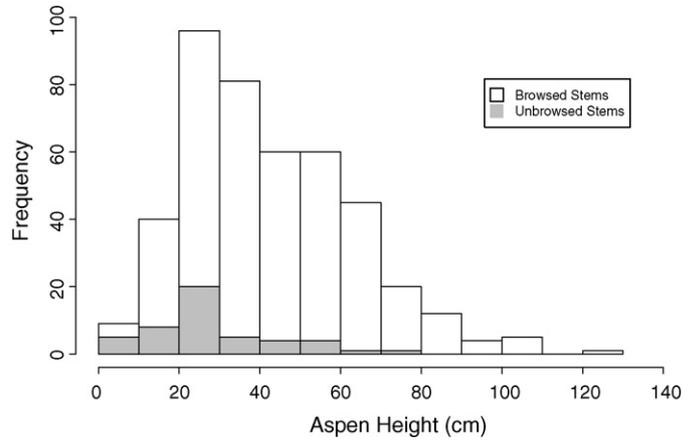

Fig. 2. Histogram of aspen seedling heights. The bar heights represent the total frequency of aspen in a given bin, while the shading shows how many of those stems were un-browsed.

sent = 325.16 stems ha^{-1}, S.D. = 718.03). The height of aspen seedlings ranged from 3 to 126 cm (mean = 42.9 cm, S.D. = 20.8, $N = 433$) and basal diameter ranged from 0.8 to 80.5 mm (mean = 12.1 mm, S.D. = 9.7, $N = 433$). In general, the aspen were short and shrubby with 89% of the individuals showing ungulate-induced browse damage (Fig. 2).

3.2. Statistical analysis

Results from the logistic regression model of pellet presence by transect (using GLMM) found that presence was not affected by the number of logs along a transect or at a site. Because number of logs was the only transect-level independent variable, we continued the analysis using standard logistic regression (in a GLM framework) and found that the only important predictor of pellet presence was distance to open areas of 1 ha or more (Table 2). However, because only 8 of 65 sites (12.3%) had zero pellets, this regression is not highly robust, and the null-model ΔAIC of 3.04 confirms that the fitted model is not substantially better than the null.

There was no relationship between pellet density and lodgepole pine sapling density at the 32 sites where sapling density was quantified. However, for the linear models

Table 2

Results from site-level model selection using standard logistic regression (GLM) and generalized least square (GLS)

Model type	Response	Sample size	Intercept	LOGSHA	HERB	DOPEN	OPEN-700	PELLETDENS	ELEVATION	WOLF	SAPLING MED	SAPLING HIGH
GLM	Pellet presence/absence	65	2.35[*]	0.0012	ns[a]	−0.0030[*]	ns	−[b]	ns	ns	ns	ns
GLS	PELLETDENS$^{1/2}$	65	13.22[***]	0.0019	ns	−0.0078[**]	ns	−	ns	ns	−3.92[**]	−0.92
GLM	Aspen presence/absence	65	18.38[*]	−8.87e−5	−0.015	ns	−12.51[*]	−0.0044	−0.0076[**]	ns	ns	ns
GLS	Aspen maximum height$^{1/2}$	31	−9.97	−1.7e−4	ns	ns	18.97[*]	ns	0.0072[*]	87.06	−1.91[*]	−0.83

Significance levels are [*]<0.05; [**]<0.01; [***]<0.001.
[a] Variable non-significant and eliminated during model selection.
[b] Variable not considered in model selection.

predicting pellet density as a function of covariates recorded for all sites, the best model selected by AIC included distance to open area, sapling impedance and the number of logs per hectare, although the latter was not statistically significant. Fewer pellets were found at sites with medium sapling impedance compared to sites with low or high sapling impedance. The model with a spherical semi-variogram fit the data better than a reduced model (ΔAIC = 10.11, likelihood ratio = 14.11, $p = 0.0009$). The estimated nugget was 0.52 and the range was 56.87 km.

We found no relationship between the number of logs along a transect and the presence of aspen seedlings. The best site-level model for explaining the presence of aspen seedlings showed that aspen were more likely to be found at lower elevations with less open meadow in the landscape (700 m buffer). Interestingly, the best linear model for explaining the maximum height of aspen seedlings at the site level shows that taller aspen are found at higher elevations with more open meadow in the landscape. There does not appear to be any spatial dependence within the residuals of this model (likelihood ratio = 4.21, $p = 0.12$). None of the covariates available were significant predictors of aspen abundance when aspen were present.

4. Discussion

Contrary to our hypothesis, our results suggest elk used regenerating forest without regard to the density of coarse wood and seemed to avoid intermediate densities of lodgepole pine saplings. Other studies (Boyce et al., 2003; Forester, 2005; Mao et al., 2005) have shown that elk use regenerating forest preferentially to other habitat types during summer. Mao et al. (2005) further demonstrated an increase in elk use of the regenerating forest following wolf re-introduction. Our initial hypothesis assumed elk would avoid areas of high impedance for energetic reasons. However, with the presence of a large predator whose primary prey is elk, these high-impedance patches may offer some protection from predation (whereas the moderate-impedance sapling stands may reduce visibility without providing physical protection). Our model for pellet abundance has spatially correlated residuals which indicates that elk are aggregating in response to factors not measured here; these could be related to the location of movement corridors or behavioral responses to broad-scale variability in factors such as forage quality, meso-topography and landscape pattern (Ripple and Beschta, 2004b).

The finding that more pellets were counted in sites close to large open areas is consistent with radio telemetry-based research (Forester, 2005; Mao et al., 2005). The sub-alpine plateaus of YNP consist of a mosaic of cover types. Of these, the open meadows have the greatest forage biomass and elk appear to select for areas of the landscape that include mixtures of regenerating forest and meadow (Forester, 2005). This selection may represent a tradeoff between meeting energetic demands and avoiding predation. Bergman et al. (2006) recently demonstrated that during winter in the Madison-Firehole region of Yellowstone, elk were less likely to be killed by wolves in burned forest. They also found that the spatial arrangement of habitats, specifically the proximity to hard edges, increased the probability of finding elk kills. This suggests that the spatial use of regenerating forest is influenced by behavioral responses to broad-scale habitat patterns rather than within-patch structure.

The increased use by elk of burned lodgepole pine stands may negate potential refugia effects of high-impedance areas and reduce the establishment likelihood of new aspen genets. Although elk tend to prefer forbs during the summer months (Canon et al., 1987; Beck and Peek, 2005), we found that nearly 90% of the aspen stems in our transects were browsed, despite the availability of alternate forage within the patches.

There may also be a conflict between conditions suitable for aspen germination and those suitable for stem growth. While we were more likely to find aspen seedlings at lower elevations and in landscapes less dominated by open meadows, the inverse relationship described the maximum height observed at a site. If aspen growth is more affected by browsing damage than length of growing season, aspen at higher elevations may grow taller due to reduced browsing pressure in the spring and fall and be less common due to a more sparse seed source. Our results are partially consistent with Romme et al. (2005). Although they observed greater mortality of seedlings at lower elevations, they found that both mortality and mean seedling height were positively related to available soil potassium. Thus, it is not surprising that we could not predict the local abundance of aspen seedlings, which tend to grow in patches and may depend more on microsite rather than broad-scale suitability.

The use of pellet counts to infer habitat use has a long history in ecology (e.g., Bennett et al., 1940; Forbes and Theberge, 1993; St-Louis et al., 2000; Ripple et al., 2001; Murray et al., 2002). While establishing a direct link between pellet density and absolute population size is difficult (Fuller, 1991, 1992; White, 1992), it is a useful technique for establishing patterns of relative areal use by animals (e.g., Palomares, 2001). One of the major hurdles associated with pellet counts is determining the age and persistence of pellet groups. This is especially important when working in areas that are high in moisture or that have large amounts of dung beetle activity, neither of which was an issue at our sites (Wallmo et al., 1962; Harestad and Bunnell, 1987; Lehmkuhl et al., 1994; Massei et al., 1998). In our study, we were able to easily distinguish between pellets that were from the current or previous summer. Because our sites were all in upland regenerating forest, variation in moisture levels among sites was low.

Ripple and Larsen (2001) used a paired design to test the mean height of aspen within and adjacent to "jackstraw" piles of coarse wood across the Northern Range of YNP. They found that the mean height of aspen growing within the jackstraw piles was significantly greater than that of the aspen adjacent to the piles (1.46 m vs. 0.54 m). Our research has shown that elk do not reduce their use of high-density accumulations of coarse wood. However, because we concentrated our research in the central plateau of YNP where aspen tend to grow very slowly (Romme et al., 2005), differences in height may be difficult to detect and confounded by abiotic and genetic factors. For

example, extreme densities of woody debris may in some cases inhibit the growth of aspen (Shepperd, 1996). Further, because coarse-wood densities and lodgepole pine saplings have grown since the 1988 fire, it is possible that the current size and spatial distribution of aspen saplings also strongly reflect browsing of new seedlings in the years prior to extensive buildup of coarse wood and saplings.

We found (off transect) one aspen sapling more than 2.5 m tall that showed very little browsing damage and was growing in a relatively low impedance area; however, numerous aspen seedlings nearby were heavily stunted by browsing. This extreme difference in both growth and apparent palatability suggests that an experimental approach that controls for local microsite characteristics (especially soil chemistry and moisture), and variability among aspen genets, should be considered before making final conclusions about the efficacy of coarse wood at protecting aspen. However, while there is no doubt that artificial log piles can be built so as to be impenetrable by elk (Ripple and Larsen, 2001), our results suggest that caution should be used when considering jackstraw piles as naturally occurring refugia.

5. Conclusions

Our results suggest that elk are relatively insensitive to accumulations of coarse wood in the landscape. Browsed aspen were ubiquitous, and aspen did not seem to benefit from a coarse-wood-induced refugia effect. However, the pellet distribution did show patterns of habitat use consistent with radio-telemetry studies (i.e., reduced use of areas far from open habitat), and aspen were less likely to be found in areas known to be preferred by elk. Although coarse wood may occasionally accumulate in densities sufficient to exclude elk at very fine scales, the probability of such accumulations coinciding with a successful aspen seedling or ramet appears to be low. Thus, it is unlikely that coarse wood will contribute to broad-scale aspen establishment in the landscape of central Yellowstone National Park.

Acknowledgements

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