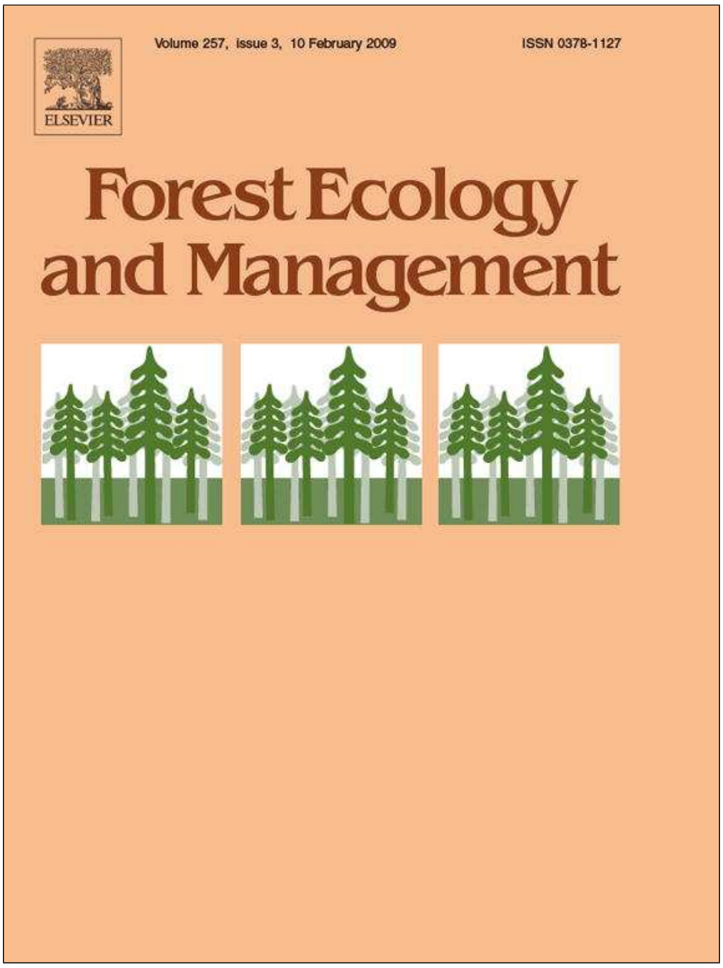
Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



Volume 257, Issue 3, 10 February 2009 ISSN 0378-1127

ELSEVIER

Forest Ecology and Management

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Forest Ecology and Management 257 (2009) 1053–1062

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Trophic consequences of postfire logging in a wolf–ungulate system

M. Hebblewhite [a,*], R.H. Munro [b], E.H. Merrill [b]

[a] Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, College of Forestry and Conservation, University of Montana, 32 Campus Drive, Missoula, MT 59812, United States
[b] Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

ARTICLE INFO

Article history:
Received 25 August 2008
Received in revised form 7 November 2008
Accepted 11 November 2008

Keywords:
Forage
Fire
Habitat selection
Salvage logging
Postfire logging
Trophic cascade

ABSTRACT

Controversy surrounds postfire logging, often because of negative effects on snag-dependent wildlife species. Few studies, however, have examined effects on early-seral species that may benefit from postfire logging, nor effects on trophic relationships. We studied the effects of postfire logging on trophic dynamics between wolves (*Canis lupus*), three ungulate species and ungulate forage biomass during the first 3 years in a large burn in the Canadian Rockies, Alberta, Canada. We examined plant biomass and ungulate responses to two treatments (post- and prefire logging) compared to a burned but unlogged area (control). We evaluated resource selection for the three treatments by elk (*Cervus elaphus*) using radiotelemetry and for deer (*Odocoileus* spp.), moose (*Alces alces*), and, secondarily, elk using pellet counts. Elk resource selection was modeled as a function of the trade-off between wolf predation risk and herbaceous forage biomass to test for trophic impacts of postfire treatments. Postfire logging had transient effects on total herbaceous biomass; while forb biomass was reduced, increases in graminoid biomass more than compensated by the third year. Prefire logging areas were dominated by a few species, but had generally higher forage biomass by the third year. Ungulates avoided postfire and prefire logged areas despite greater herbaceous biomass. Only when we considered elk resource selection as a function of both forage and wolf predation risk was the extent to which trophic interactions affected by postfire logging revealed. Wolves selected proximity to roads and the higher forage biomass associated with postfire logging in open logged areas. This translated to the highest predation risk for elk in postfire logged areas. Thus, ungulates avoided postfire logged areas because of human alteration of top-down predation risk despite enhancements to bottom-up forage biomass. Managers should consider trophic consequences of postfire logging on the interactions among species when gauging logging effects on terrestrial ecosystems. Making use of existing roads, minimizing the construction of new roads, and managing road removal following postfire logging will help mitigate the negative effects of postfire logging on terrestrial ecosystems.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

Postfire logging has emerged as one of the most important international controversies in fire-management in recent decades (Schmiegelow et al., 2006; Lindenmayer and Noss, 2006; Hutto, 2006; Noss and Lindenmayer, 2006; Lindenmayer et al., 2008). Research on the effect of postfire logging in Australia on endangered arboreal marsupials clearly demonstrated its negative impact, generating national debates on postfire logging practices (Lindenmayer et al., 2008). And in North America, the recent debate regarding political interference in the science of postfire logging in Oregon 'fuelled the fire', elevating the issue of postfire logging to the international level (Stokstad, 2006; Baird, 2006; Dellasala et al., 2006; Donato et al., 2006a, b). Given that climate change may increase the frequency of wildfires in western North America (Brown et al., 2004), demands for postfire logging will likely increase, making the need to resolve this debate paramount. In the debate about postfire logging, disruption of postfire ecosystem processes is considered the main issue (Hutto, 2006; Noss and Lindenmayer, 2006; Lindenmayer and Noss, 2006). These ecosystem processes include fuel accumulation, hydrology, sediment transport, forest regeneration, as well as species movements and recolonization dynamics following fire. Numerous recent studies have demonstrated that postfire logging increases sediment load in watersheds, soil erosion, reduces seedling regeneration, and increase fire fuels and that the effects of postfire logging are critically dependent on the complexities of the prefire environment and postfire treatment (McIver and Starr, 2000; Beschta et al., 2004; Karr et al., 2004; Donato et al., 2006a,b).

---

* Corresponding author. Tel.: +1 406 243 5521; fax: +1 406 243 4845.
E-mail address: mark.hebblewhite@umontana.edu (M. Hebblewhite).

0378-1127/$ – see front matter © 2008 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2008.11.009

Author's personal copy

From a wildlife perspective, postfire logging removes critical habitat for snag-dependent and cavity-nesting species such as mountain bluebirds (*Sialia currucoides*), black-backed (*Picoides arcticus*), hairy (*Picoides villosus*), and three-toed woodpeckers (*Picoides tridactylis*) (Hutto, 1995; Hobson and Schieck, 1999; Hoyt and Hannon, 2002), long-legged Myotis (*Myotis volans*) (Baker and Lacki, 1998; Fisher and Wilkinson, 2005) in western North America, as well as arboreal marsupials in Australia (Lindenmayer et al., 2008). The effects of postfire logging may vary, however, negatively impacting late-succession species or positively affecting early-seral species, as evidenced by studies of ground dwelling beetles in the boreal forest following postfire logging (Koivula and Spence, 2006; Phillips et al., 2006). Early-seral ungulate species such as moose (*Alces alces*), elk (*Cervus elaphus*), mule (*Odocoileus hemionas*) and white-tailed deer (*Odoicoleus virginianus*) may benefit from fire because they consume plant species that increase following fire (Peek, 1974; Merrill et al., 1982; Smith, 2000), which may translate to demographic benefits (Boyce and Merrill, 1991; Taper and Gogan, 2002). Unfortunately, few if any studies have explicitly examined effects of postfire logging on ungulates (McIver and Starr, 2000). Forage biomass for ungulates was enhanced more after fires in closed forest stands more than open habitats in the Canadian Rockies (Sachro et al., 2005) because fires removed stand structure, increasing solar insolation and nutrient availability to forage plants (Van Dyke and Darragh, 2007). Similarly, postfire logging may also increase forage biomass because of stand removal. Indeed, benefits to early-seral species are often voiced as arguments promoting postfire logging, though scant data support this hypothesis.

Despite the potential forage benefits, postfire logging removes hiding cover provided by burned snags, and the importance of hiding cover for ungulates has been known for decades (Lyon, 1983; Rowland et al., 2000). Hiding cover is important because ungulates must balance benefits from forage with the risk of predation and often use cover to evade predation (Pulliam, 1989; Pierce et al., 2004; Frair et al., 2007). Postfire logging may increase predation risk by humans or non-human predators because reduced cover may increase vulnerability to predation (Hebblewhite et al., 2005) and because of the road networks used for postfire logging—a key difference from burned and unlogged areas with few roads. Enhanced vulnerability of elk to human hunting on roads has also been known for decades (Lyon, 1983; Rowland et al., 2000). Recent studies also show wolf (*Canis lupus*) predation risk also increases near roads for elk (Hebblewhite et al., 2005), moose (Kunkel and Pletscher, 2000), and woodland caribou (James and Stuart-Smith, 2000). While few studies have explicitly examined impacts of postfire logging roads on ungulates, we expect similar responses of elk to roads associated with postfire logging. Furthermore, if postfire logging enhances forage biomass relative to burned stands, we may expect predators to select postfire logged stands because predator–prey theory predicts predator distribution will match the distribution of the food of their prey (Lima, 2002; Luttberg and Sih, 2004). Thus, reductions in hiding cover, enhanced predation risk due to roads, and habitat selection of predators themselves may affect ungulate responses to postfire logging as much as potential bottom-up effects. Unfortunately, few if any studies have examined the trophic consequences of postfire logging.

Therefore, the goal of this study was to investigate the trophic consequences of postfire logging in a wolf–ungulate–plant system. We conducted our study within the 11,000-ha Dogrib fire of August 2001 in the upper foothills of the Canadian Rockies in Alberta, Canada, taking advantage of previous research in the larger landscape surrounding this burn on wolves and elk to address the trophic impacts of postfire logging. Following the fire, the burn was a patchwork of sites that were burned and unlogged (58%), burned and logged the winter following fire (postfire logged, 25%), and logged within 20 years prior to the fire and burned (prefire logged, 17%). Specific objectives of the study were to compare the effects of the two treatments (postfire and prefire logged) versus an unlogged, burned control on (1) herbaceous forage biomass between treatment types, (2) resource selection by three ungulate species (elk, deer, and moose) for the different treatment types, and finally, (3) resource selection by elk for forage biomass and wolf predation risk within the burn (Hebblewhite and Merrill, 2007, 2008). We first tested how the three treatment types changed ungulate forage biomass, and what landscape factors influenced postfire vegetation. With an understanding of how the forage resource changed following postfire logging, we then tested whether elk resource selection was driven by bottom-up (forage biomass) or top-down (predation risk) processes by examining elk resource selection as a function of treatment type, forage biomass and predation risk. If postfire logging increased forage biomass, and if bottom-up effects of forage were more important in determining elk resource selection than predation risk, then we predicted that elk would show strong selection for postfire logged areas. Alternately, if wolf predation risk was higher in postfire logged areas than controls, and if top-down processes drove elk resource selection, then we predicted elk would avoid postfire logged areas.

2. Methods

2.1. Study area

The Dogrib fire occurred in west-central Alberta (51°38′–115°30′), Canada, adjacent to Banff National Park (BNP) (Fig. 1). The burn straddled the upper foothills and montane ecoregions, with elevations ranging from 1500 to 2350 m. Climate for the study area was cold continental, with long cold winters and short summers. Winter (November–April) precipitation was an average of 54 cm total snowfall, and summer (June–August) precipitation averaged 260 mm from 1962 to 2004 (Bluehill tower weather station, Environment Canada). The area was home to diverse, but generally low density, ungulate community, including elk, white-tailed deer, mule deer, bighorn sheep (*Ovis canadensis*) and feral horses (*Equus caballus*). Our study focuses on summer use of postfire landscapes because ungulate use of the Dogrib burn was concentrated during summer, while elk and other ungulates migrated to winter ranges outside the Dogrib burn. Wolves were the main predators of ungulates in the study area, but other predators included humans, grizzly bears (*Ursus arctos*), cougars (*Felis concolor*), and coyotes (*Canis latrans*), in order of importance for elk (Hebblewhite, 2006). See Hebblewhite et al. (2006) for more details on the study area.

Human activity in the study area was concentrated on roads, seismic lines and trails and included off-road vehicle use, hiking, and vehicle traffic, and peaked during the hunting season during which most road and seismic lines received human activity. All ungulate species and wolves were subject to general liberal harvest seasons in the study area. Road networks were concentrated in logging areas in lower to mid-slopes as the surrounding area was entering first full rotation in the local forest harvest plan. Forest roads were concentrated in the central and eastern part of the study area; the western half of the Dogrib fire was in an unroaded wilderness area. Road densities were higher in the Dogrib burn than adjacent areas (mean road density in burn was 1.5 km/km^2, whereas in a 5 km buffer surrounding the burn, road density was 0.2 km/km^2).

Author's personal copy

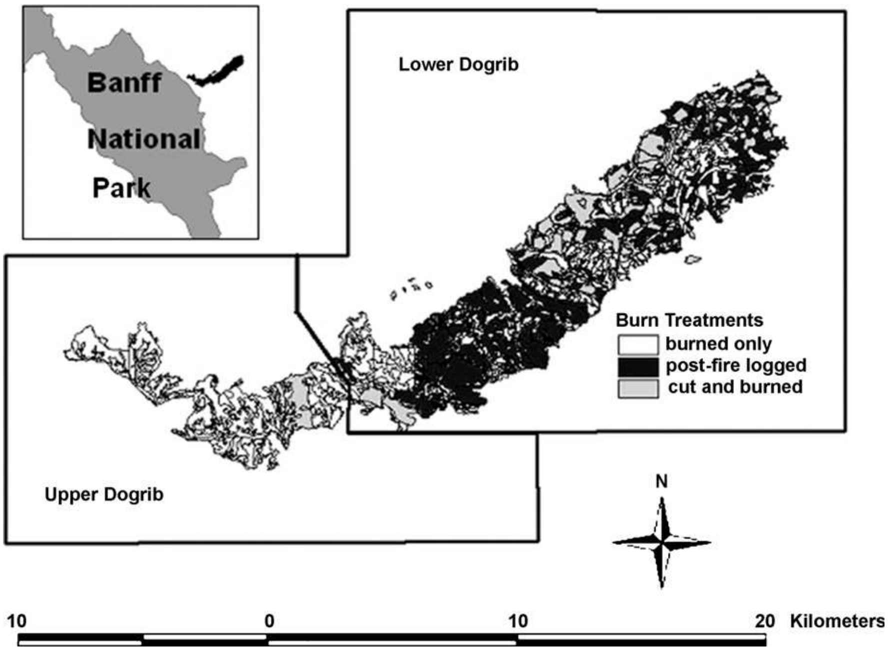


Fig. 1. Postfire landscape treatments within the Dogrib burn including burned, postfire logged, and prefire logged treatments. Inset shows location of the Dogrib burn with respect to Banff National Park in Alberta, Canada (Latitude 51°38′ Longitude 115°30′).

2.2. The Dogrib fire

The Dogrib burn was classified as a crown-sustained human-caused fire (Alberta Sustainable Resources Development, AB-SRD, *unpublished data*) and burned 10,200 ha between 10 September and 16 October 2001. Using the normalized burn ratio of Key and Benson (2003), an index derived from remote sensing based on visible crown mortality (see Section 2.3 for more detail), the median fire severity was 0.69 (on a scale of 0–1) and 78% of the fire was classified as a high severity burn. The upper elevation, western portion of the burn prior to the burn was comprised of lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea englemanni*), grading to white spruce (*Picea glacua*) at lower elevations, interspersed with shrub meadows (*Salix* spp. and *Betula glandulosa*), grasslands, and alpine herbaceous communities. The eastern and lower elevation Dogrib burn prior to the burn was comprised of lodgepole pine and white spruce, black spruce (*Picea mariana*)/ tamarack (*Larix laricna*) bogs, riparian areas, and trembling aspen (*Populus tremuloides*) stands. Within the boundary of the burn (Fig. 1), a patchwork of two treatments and an unlogged 'control' treatments occurred, including (1) burned and unlogged (control—55%), (2) postfire logged (24%), and (3) prefire logged areas that were harvested ≤20 years prior to the Dogrib burn (16%) (Fig. 2). Logging all occurred during winter months when ground was frozen, and was generally done on slopes <30° using feller bunchers, skidders and road networks, and on slopes >30° using cable logging following guidelines developed by Alberta Forestry for postfire logging. Postfire retention of trees or snags was extremely low; essentially all timber was removed, with retention <5% (e.g., Fig. 2). Mean postfire cutblock size was 19 ha with a maximum postfire logging block size of 246 ha, twice that of logged and burned areas (e.g., Fig. 1). We obtained spatial coverage's of the different treatment areas from Sundre Forest Products Ltd.

Because natural disturbances are unpredictable and unplanned, it is usually difficult to study their effects with strong pre- and post-disturbance experimental designs (Bennett and Adams, 2004; Wiens and Parker, 1995). Furthermore, true replicates are often not possible because the only true level of independent replication is the disturbance event itself, in our case, the entire Dogrib burn. We believe, however, that if interpreted cautiously, comparison of postfire vegetation dynamics among the management treatments within the Dogrib burn is a valid method for studying effects of disturbance, despite the lack of prefire control information. In this context, evaluation of the Dogrib burn represents a 'management experiment' at a useful spatial and temporal scale to provide guidance for land management in similar areas and postfire logging treatments. Thus, our results may not directly relate to areas with stricter regulations regarding postfire retention, although there is currently no policy regarding this in Alberta.

2.3. Elk forage abundance

We used a proportional allocation random stratified sampling design (Krebs, 1989) to sample forage biomass using spatial geographic information system (GIS) layers of the four main strata. We acknowledge the importance of forage quality to ungulates (Hebblewhite et al., 2008), but here, focused only on postfire changes in forage abundance. We determined random sampling locations (sites) within potential strata combinations using ARCView 3.2 (ESRI) to sample 30-m transects (the site) within: (1) the two postfire treatments (post- and prefire logged) and in the burned and unlogged control treatment; (2) slope categories of flat (0–5°), moderate (5–30°), and steep (>30°); (3) aspect classes of north (0–112.5° and 292.5–360°), south (112.5–292.5°), and flat (overlapping with flat slopes), and to facilitate economic sampling, (4) areas within 1 km of a road to facilitate economic sampling. Thus, each site (transect) was the sample unit for vegetation sampling. Our initial design focused on postfire logged and the burned and unlogged (control) treatments because we did not originally recognize the importance of the prefire logged treatment until the second-year. Thus, in 2003, we added the prefire logging treatment. A post hoc ANOVA between treatments for systematic differences in fire severity, elevation, aspect and slope confirmed transects were randomly allocated with no systematic differences in landscape covariates that may have influenced results (Table S1, supplementary materials).

Author's personal copy

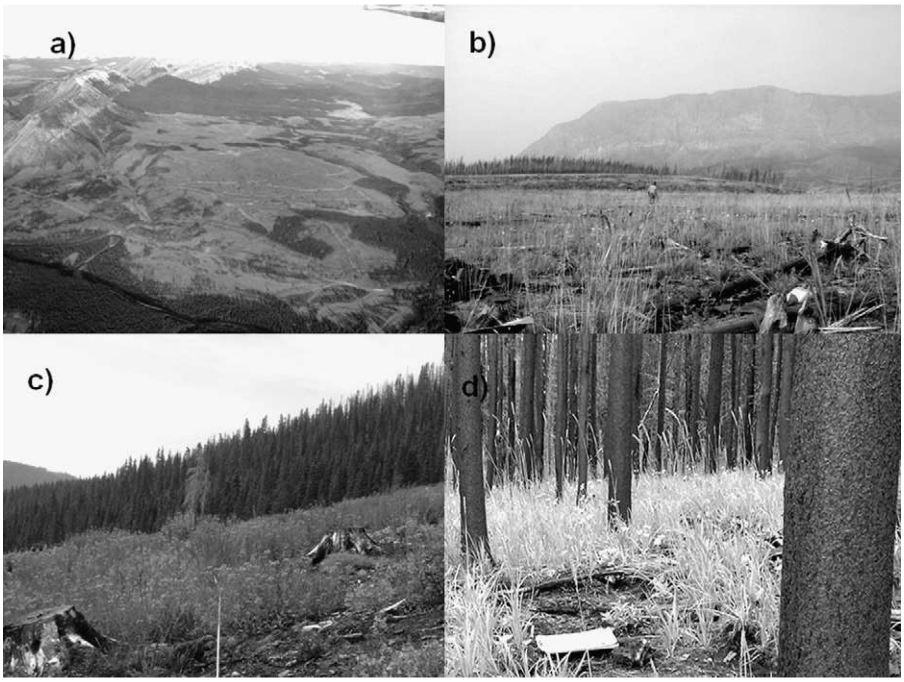


Fig. 2. Photographs depicting (a) an aerial oblique photograph of the central portion of the Dogrib burn where the largest concentration of postfire logging occurred, including a 240 ha postfire logged cutblock, (b) a representative postfire logged site representative of the low level of retention, (c) a prefire logged site showing stumps from trees cut before the fire, and (d) a burned but unlogged, control site for reference. All photos were taken in summer 2003.

We sampled herbaceous forage biomass during the peak of the growing season during July and August 2002–2004. We sampled 7–8 sites in each of 2 treatments (burned, postfire logged) in 2002, 22–28 sites in each of the 3 treatments (burned, post- and prefire logged) in 2003, and 19–22 in each of 2 treatments (burned, postfire logged) again in 2004. We focussed on herbaceous forage because differences in diet quality for elk were driven by herbaceous, not shrub, biomass (Hebblewhite et al., 2008). Shrub cover was insufficient post-burn to warrant measurement from a hiding cover perspective. We estimated the relative abundance of forage classes (forb, graminoid) and key species based on cover (%) within five 1-m^2 plots at each site along a 30 m transect. We measured total herbaceous biomass by clipping to 2 cm all standing herbaceous biomass (recording % of green and dead biomass) within three plots, and weighing oven-dried samples (50° for 48 h) to the nearest 0.1 g. We calculated the biomass of each forage class at a site based on the total biomass and relative cover values of each forage category, but report only green biomass in g/m^2 of dry matter because green biomass is critical for summer nutrition (Hebblewhite et al., 2008).

We compared site differences in forage components (total green herbaceous, forb, and green graminoid biomass, hereafter referred to as total, forb, and graminoid) in the first three growing seasons after the burn between sites that were burned (control) and postfire logged (treatments) using a two-factor ANCOVA design for each forage biomass as a dependent variable and with year and treatment type as main effects in STATA 9.0 (StataCorp, 2003). While we resampled plots between years, unbalanced sampling prevented use of a repeat measures design because not all sites were resampled in each year because of logistical difficulties. To test the hypothesis of treatment differences over time we included a treatment × year interaction, and investigated significant differences in main effects using Tukey's HSD post hoc tests (Sokal and Rohlf, 1995). We transformed forage biomass using a natural logarithm (ln+0.5) transformation to satisfy normal distribution assumptions of ANCOVA to accommodate sites with zero biomass. We tested for normality using Levene's test (Sokal and Rohlf, 1995). For data collected in across three treatment types (burned, post- and prefire logged), we used a one-way ANCOVA on similarly transformed data with treatment as a main fixed effect. To minimize the risk of Type II error, we set alpha at 0.10 for ANCOVA models, and all tests were evaluated as two-sided tests.

We controlled for effects of landscape covariates (elevation, fire severity, soil wetness, slope, aspect) in the ANCOVA models. We screened for collinearity in landscape covariates using a threshold of $r = 0.5$ to exclude correlated variables. We calculated topographic landscape covariates using a 30-m resolution digital elevation model. Topographic covariates included elevation (m), slope (degrees), aspect, hillshade (evaluated at 45° inclination at an aspect of 225° to represent xeric sites with high values, and mesic sites with low values, and a soil moisture index (compound topographic index, CTI (Gessler et al., 1995). We also calculated fire severity using a remote sensing approach following the normalized burn ratio of Key and Benson (2003) derived from LANDSAT 5/7 images obtained before (7 September 1998, Path 43/Row 24, LANDSAT 5) and after (22 June 2002, LANDSAT 7) the Dogrib burn. We followed the approach of Key and Benson (2003) in calculating the normalized burn ratio. The Dogrib burn was characterized by overall high fire severity (see Section 2.2). Finally, we calculated distance to low severity or unburned areas to provide a measure to index potential seed sources for postfire vegetation recovery (Turner et al., 1994). We defined low or unburned areas using a fire severity of 0–0.45 (see Section 2.2) using the Jenks natural breaks clustering algorithm in ArcGIS 9.0 (ESRI). We then combined low severity areas and surrounding unburned forest matrix and calculated distance to this combined layer to assess the effects on forage biomass recovery following fire.

2.4. Wolf predation risk

We used a wolf predation risk model (Hebblewhite and Merrill, 2007, 2008) previously developed for a much larger study area to determine risk within the Dogrib burn specifically to test a novel

Author's personal copy

hypothesis about postfire logging and trophic dynamics. Elsewhere, we tested hypotheses about migration and landscape-scale resource selection using this predation risk model (Hebblewhite and Merrill, 2007, 2008). Here, our goal was to examine the trade-off between risk and forage just within the postfire Dogrib burn treatments. To determine predation risk, briefly, we estimated summer resource selection functions for wolves using GPS locations ($n = 12{,}521$) from 15 GPS collared wolves from all packs overlapping the Dogrib burn during 2002–2004. Predation risk was modeled by combining wolf resource selection with the spatial density of wolves, weighted by wolf pack size (Hebblewhite and Merrill, 2007). Wolf resource selection was modeled using mixed-effects resource selection function (RSF; Manly et al., 2002; see below) models that allowed for heterogeneity in resource selection for human activity (Hebblewhite and Merrill, 2008). We tested for differences in total predation risk between sampled vegetation plots using ANOVA (following methods described above for forage) to test whether wolf predation risk differed between treatments. To understand the mechanism driving wolf selection for treatments within the Dogrib burn, we report coefficients of selection for forage biomass and human activity such as logging roads here from Hebblewhite and Merrill (2007, 2008).

2.5. Ungulate resource selection

We assessed resource selection by the three main ungulate species (deer, elk and moose) during summer (June, July and August) within the Dogrib burn using pellet counts, and in more detail just for female elk with telemetry data. Criticisms of pellet counts are that pellet counts are unrelated to density (Fuller, 1991), and biases such as differential detection and decomposition rates (Brodie, 2006) in different landcover types reduce pellet counts utility. We felt these problems were reduced in our study because of the short duration since the burn (during which all older pellets were consumed), the arid environment enabling long pellet persistence, and the point that our study was not looking at modeling density, merely spatial distribution, which previous reviews supported pellet counts as a measure of (Neff, 1968). Furthermore, for elk, we used both telemetry and pellet counts, allowing a comparison between methods to evaluate these potential biases. Ungulate pellet groups per unit area (pellet groups/m^2) from summer (defined as fresh pellet groups only since June) for elk, moose and deer spp. (mule deer and white-tailed deer pellets were indistinguishable) were counted within a 300-m^2 rectangle along each 30-m transect. Because ungulate pellet counts followed a negative binomial distribution (Hilbe, 1999), these data were analyzed with negative binomial regression using NBREG in STATA 9.0 (StataCorp, 2004). We tested for fit of the negative binomial model versus the Poisson or zero-inflated negative binomial model using the likelihood ratio and Vuong test (Hilbe, 1999), which confirmed negative binomial models were the most appropriate (all LR test and Vuong test P-values < 0.0005). The main treatment and year effect were entered into the model using indicator coding. Although we considered the same landscape covariates as listed above in the final model, we do not report them here because none were statistically significant.

For the second resource selection analysis using elk telemetry data for just adult female elk, we considered treatment types as well as forage biomass and wolf predation risk. We used telemetry location data for 2002–2004 from Global Positioning Systems (GPS) collars (LOTEK GPS3300, Aurora, ON) and standard VHF collars (LOTEK, LMRT-4 collars) on female elk captured during winter at the Ya Ha Tinda winter range; see Hebblewhite et al. (2006) for capture and handling details (all captures were conducted according to an approved University of Alberta and Parks Canada animal care protocol). VHF collared elk were located every 7–14 days via ground or aerial telemetry, and GPS collars obtained a location every 2 h. GPS-bias was low enough to be ignored (Hebblewhite et al., 2007). We sampled availability of resources to elk using a balanced number of used and available points with a minimum of 100 random points for each elk within the Dogrib burn.

We developed resource selection functions (RSF; Manly et al., 2002) within the Dogrib burn considering selection simultaneously for forage biomass, predation, and their interaction while accounting for the three treatment classes. We evaluated resource selection using the use-available design of Manly et al. (2002) where covariates at used and random locations were contrasted to estimate:

$$\hat{w}*(x) = \exp(\hat{\beta}_1 F + \hat{\beta}_2 P + \hat{\beta}_n F * P + \mathbf{B}_x \boldsymbol{X}) \tag{1}$$

where $\hat{w}*(x)$ is the relative probability of use as a function of the coefficients $\hat{\beta}$ of forage (F), predation (P), and their interaction (F^*P), and $\mathbf{B}_x\mathbf{X}$ is the vector of coefficients of categorical treatment types estimated from fixed-effects logistic regression (Hosmer and Lemeshow, 2000; Manly et al., 2002) in Stata 9.0 (StataCorp, 2004). We interpret selection for a particular treatment if $\hat{\beta}$ for the categorical treatment was positive, and avoidance if $\hat{\beta}$ was negative, reflecting use that was greater or less than expected based on availability, respectively (Manly et al., 2002). We screened for collinearity in independent variables using a threshold of $r = 0.5$ to exclude correlated variables and assessed whether variables were confounded using the guidelines of Hosmer and Lemeshow (2000); no covariates were confounders of the relationship between treatments and elk selection. See below for a description of how forage and predation risk covariates were calculated. Random effects were included for individual elk to control for heterogeneity in resource selection between elk and unbalanced sampling designs common when combining VHF and GPS datasets using GLLAMM in Stata 9.0 (Skrondal and Rabe-Hesketh, 2004; Gillies et al., 2006).

We considered linear, quadratic and fractional polynomial (Hosmer and Lemeshow, 2000) terms for predation and forage (e.g., to test for intermediate forage biomass selection *sensu* Hebblewhite et al., 2008). The top model from the all-inclusive simple candidate set of forage, predation, their interaction, etc., was selected using AIC$_c$ where n was considered the number of elk (Burnham and Anderson, 1998). Predictive capacity of the top RSF model was assessed using k-folds cross-validation (Boyce et al., 2002).

Forage abundance at each telemetry and random point was estimated based on the approach developed by Hebblewhite et al. (2008), which we briefly outline here. Over a much larger study area (10,000 km^2) containing the Dogrib burn, we used stratified-random sampling to sample availability of herbaceous forage biomass (following similar methods as above) near the peak of the growing season (4 August) within landcover types and an index of primary productivity, NDVI (the normalized difference vegetation index) from the MODIS satellite. By correlating peak forage biomass at a site to NDVI from MODIS satellites and other landscape covariates (which explained $>$70% of the variance in forage biomass at a site), we statistically modeled the peak of herbaceous forage (g/m^2) across the study area within the Dogrib burn. See Hebblewhite et al. (2008) for more details on methods.

3. Results

3.1. Forage differences between treatments

The ANCOVA model testing for differences in total herbaceous biomass (forb + graminoid) between burned and postfire logged

Author's personal copy

sites across 3 years was significant ($F_{6,99} = 14.74$, $P < 0.0005$), and explained 47% of the variance (Fig. 3). Although total herbaceous biomass increased over time ($F_{2,99} = 39.9$, $P < 0.0005$, Fig. 3), there was no statistical effect of treatment on herbaceous biomass ($F_{1,99} = 1.23$, $P = 0.27$), and no interaction ($F_{2,99} = 1.71$, $P > 0.50$). Only by the third year was a difference evident such that total biomass was higher in postfire logged sites (Fig. 3, Tukey's HSD *P*-value <0.03). The only landcover covariate to influence total herbaceous biomass over the 3 years was hillshade ($F_{1,99} = 3.65$, $P = +0.06$), with higher biomass in more xeric sites (Regression coefficient, $\beta = +0.014$, S.E. = 0.007). Differences in total forage biomass at burned, postfire, and prefire logged sites in 2003 were not statistically significant ($F_{3,52} = 2.04$, $P = 0.12$), and the ANCOVA model explained only 12% of the variance. Although treatment type did not have a significant impact on herbaceous biomass, both the burned control and prefire logged sites had more biomass than postfire logged areas (Fig. 3). During the three treatments comparison in 2003, fire severity reduced total herbaceous biomass ($F_{1,52} = 4.32$, $P = 0.04$, $\beta = -3.9$, S.E. = 1.87).

The forb ANCOVA model explained 51% ($F_{5,97} = 14.62$, $P < 0.0005$) of the variance in forb biomass. Postfire logging reduced forb biomass consistently across all 3 years compared to burned only sites ($F_{1,97} = 3.29$, $P = 0.07$, Fig. 3), but the differences were significant only in the first 2 years post-burn (Tukey's HSD test $P < 0.04$). There was no interaction between treatment and year ($F_{2,97} = 1.70$, $P = 0.19$). Forb biomass increased over time ($F_{2,97} = 30.92$, $P < 0.0005$). The only landcover covariate that influenced forb biomass from 2002 to 2004 was north facing slopes ($F_{2,97} = 2.95$, $P = 0.07$), where forb biomass was reduced ($\beta = -1.1$, S.E. = 0.47). The forb biomass model for 2003 treatment differences was significant ($F_{2,74} = 6.00$, $P = 0.004$) but only explained 14% of the variance in forb biomass. Postfire logging reduced forb biomass during 2003 compared to both burned and prefire logging treatments ($F_{2,74} = 6.00$, $P = 0.004$), which post hoc tests revealed were not statistically different (postfire

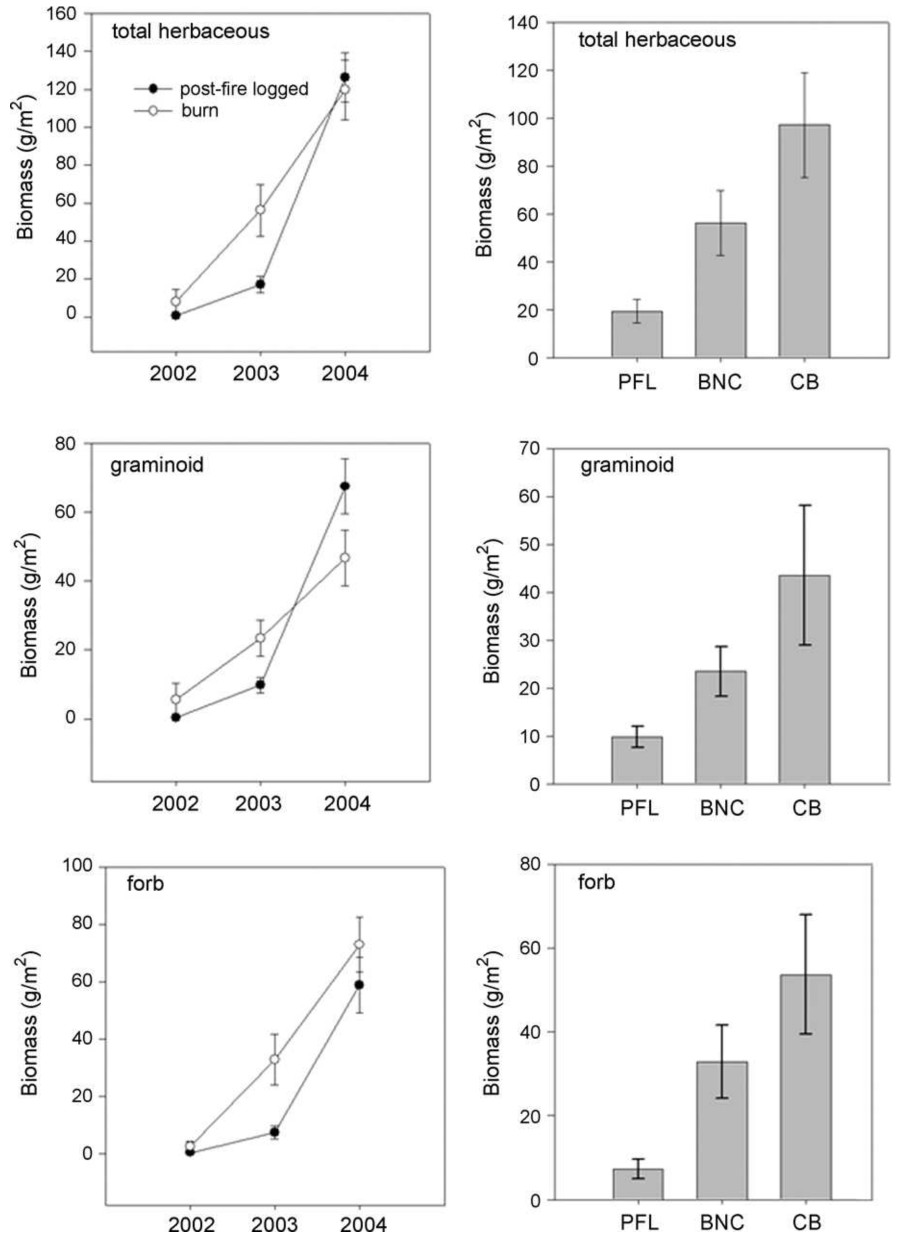


Fig. 3. Responses and 95% confidence intervals of total herbaceous, forb, graminoid, and shrub biomass (g/m^2) to (a) postfire logged (●) and burned (○) treatments in the first 3 years post-burn 2002–2004, and to (b) postfire logged (PFL), burned (BNC) and prefire logged (CB) treatments just in 2003.

Author's personal copy

logging $<$ burned = prefire logging, Fig. 3). No landcover covariates were statistically significant during the 2003 comparisons.

The graminoid biomass model fit well ($F_{6,99} = 10.87$, $P < 0.0005$) and explained 40% of the variance. While treatment type did not have a main effect on graminoid biomass ($F_{1,99} = 0.18$, $P = 0.67$), the effect of treatment interacted with year such that postfire logging reduced graminoid biomass in 2002 and 2003, but graminoid biomass was higher in postfire logged sites in 2004 ($F_{2,99} = 3.12$, $P = 0.05$). Similar to total herbaceous biomass, hillshade increased graminoid biomass significantly in more xeric sites ($F_{1,99} = 7.88$, $P = 0.06$, $\beta = +0.022$, S.E. = 0.008). During just 2003, the ANCOVA model was significant ($F_{3,52} = 3.29$, $P = 0.03$), but only explained 14% of the variance in total herbaceous biomass, which did not differ between any of the three treatments ($F_{2,52} = 0.18$, $P = 0.83$). Fire severity was important in reducing graminoid biomass in 2003 ($F_{1,52} = 9.0$, $P = 0.003$, $\beta = -5.9$, S.E. = 1.9).

3.2. Wolf predation risk

Wolf predation risk was a function of resource selection by wolves for roads, edge habitats, landcover types that contained high forage biomass for ungulates (grasslands, shrub meadows, etc.), and lower elevations (Hebblewhite and Merrill, 2008). Moreover, wolf predation risk was strongly influenced by proximity to active wolf dens (Hebblewhite and Merrill, 2007). The main wolf pack whose territory encompassed the Dogrib burn, the Wildhorse pack, selected areas closer to roads (coefficient from a conditional RSF model of summer wolf selection for distance to road, $\beta = -0.20$, S.E. = 0.03, Hebblewhite, 2006), and showed strong selection for areas with higher total herbaceous forage biomass (coefficient for selection for forage biomass, $\beta = +0.015$, S.E. = 0.001). Within the burn, predation risk was the highest at sampled vegetation plots in postfire logged areas (relative predation risk value = 5.3, Table 1), intermediate in pre-logged areas (wolf predation risk = 5.1), and lowest in burned, unlogged areas (wolf predation risk = 4.7), a total difference of about 17% between postfire logged and burned areas (overall ANOVA $F_{2,130} = 51.4$, $P < 0.005$).

3.3. Ungulate resource selection

Moose pellet groups (0.06 pellets/300 m^2, S.E. ± 0.05) were lower than elk (0.25, S.E. ± 0.05) or deer (0.24, S.E. ± 0.05) across the burn. Negative binomial models indicated that for all three ungulate species, pellet counts were lower in the postfire logged treatment than either burn or logged and burn (Table 2). Elk pellet counts were lower than burned sites in postfire logged sites, and higher in the prefire treatment (Table 2). There was no significant difference in deer pellet groups between prefire logged sites, but they were significantly lower in postfire logged sites (Table 2). Moose pellet counts were low and variable in all sites, and there were no significant differences between sites owing to low moose pellet counts (Table 2).

We collected a total of 186 VHF telemetry locations from 21 VHF-collared elk, and 2068 GPS telemetry locations from 10 GPS-collared elk. Because of the imbalance in VHF and GPS samples, we performed RSF analyses with both and just the GPS data, but noted no differences in results, so report only the combined VHF and GPS data here (M.H., unpublished data), accommodating for the sample unit of individual elk as explained in the methods. Although use of the Dogrib burn by elk increased during the 3 years' post-burn (2002 = 12% of all collared elk, 2003 = 23%, 2004 = 32%), and peaked in July (35% of all summer telemetry locations), use remained almost exclusively in the western portion of the burn. The top resource selection model was a function of treatment type, predation risk and forage biomass, without a predation–forage interaction or non-linear effects (Table 2). We considered only the top RSF model because the ΔAIC for the second ranked model was $>$500 units. The probability of elk use of an area once it was within the Dogrib burn increased with increasing forage biomass ($\beta = +0.018$), decreased with increasing predation risk ($\beta = -0.80$), and was similarly lower for both postfire logged ($\beta = -3.48$) and prefire logged areas ($\beta = -3.37$) than the reference category which was burned habitats (Table 2). The *k*-folds cross-validation of the top model had a spearman rank correlation between predicted and observed $r_s = 0.96$ (S.E. = 0.005), confirming excellent predictive capacity. Selection coefficients for treatment type was negatively correlated with average wolf predation risk for each treatment type (Table 2), confirming that postfire logging stands had the highest predation risk and elk strongly avoided these stands. Solving for the relative predicted probability of use as a function of treatment type and forage biomass shows that elk consistently selected post- and prefire logged areas less than burned only areas (Fig. 4).

Table 1
Model structure for the top-ranked generalized linear mixed-effects resource selection function (RSF) model for the relative probability of elk use of the Dogrib burn, Alberta, 2002–2004.

Parameter	Coefficient	S.E.	Wolf predation risk[a]	S.E.
Constant (burned reference category)	−6.56	0.470	4.63	0.24
Postfire logged	−3.48	0.235	5.31	0.15
Prefire logged	−3.37	0.291	5.12	0.09
Wolf predation risk	−0.799	0.041	–	–
Herbaceous biomass (g/m^2)	0.017	0.0009	–	–

For comparison, the average wolf predation risk in the three treatment types from ANOVA are shown for postfire logged, prefire logged, and burned (reference) categories. See text for details.

[a] Calculated from Hebblewhite and Merrill (2007).

Table 2
Negative binomial regression parameter estimates (S.E.) for the effects of postfire treatment categories on pellet group counts for elk, deer spp., and moose from the Dogrib burn, 2002–2004.

Species	β_0[a]	Postfire logged	Prefire logged	LR χ^2, *P*-value
Elk	−**2.25** (0.504)	−**1.66** (0.67)	**1.32** (0.643)	11.59, $P < 0.001$
Deer spp.	−**0.95** (0.314)	−**0.88** (0.423)	0.14 (0.584)	18.72, $P < 0.005$
Moose	−**2.09** (0.730)	N/A	0.57 (1.301)	29.10, $P < 0.0001$

Bold indicates significant at $P = 0.10$.

[a] Note that β_0 represents the reference treatment burned and unlogged.

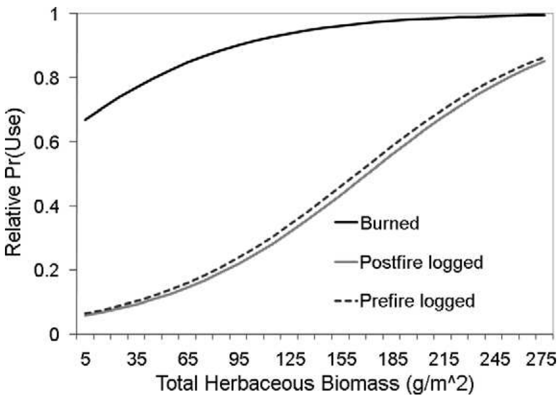


Fig. 4. Predicted relative probability of use by elk as a function of total herbaceous biomass within the three postfire treatments; burned, postfire logged, and prefire logged.

Author's personal copy

4. Discussion

Postfire logging may increase forage biomass for early-seral species such as ungulates, suggesting potential benefits from purely a bottom-up, or forage only perspective. By the third year post-burn, graminoid biomass recovered to the point where total herbaceous biomass was equal or greater in postfire logged areas. This may have been due to higher soil temperatures (e.g., hillshade covariate), greater access to sunlight, or reduced competition from regenerating conifer seedlings than in the burned areas (Donato et al., 2006a,b). While forb biomass was initially reduced by postfire logging, by the third year, the difference between burned and postfire logged stands had declined considerably. Thus, by the third year-post-burn, there were few differences between postfire logged and burned treatments from strictly an ungulate forage perspective. If there was any biological difference, postfire logged stands had higher herbaceous biomass during the third year. Plant diversity also was slightly lower (but not significantly) in prefire logged areas, and evenness, a measure of species dominance, was greater in prefire logged sites (M.H., *unpublished report*), suggesting a few species rapidly colonized prefire logged areas. Fireweed (*Epilobium* spp.) and *Calamagrostis* spp. dominated (supplementary Table S2) similar to unburned cutblock vegetation elsewhere in the foothills of the Canadian Rockies (Sachro et al., 2005). Hence, our prefire logged sites had higher forage biomass likely because dominant pre-burn plant species were characteristic of more open habitats (compared to burned forest), allowing for rapid colonization after fire, similar to Sachro et al. (2005).

The few forage differences we did observe in plant dynamics were consistent with the literature on postfire logging (McIver and Starr, 2000; Lindenmayer and Noss, 2006). Postfire logging reduced herbaceous cover in Arizona Ponderosa Pine (*Pinus ponderosa*) stands (Blake, 1982). In Oregon Ponderosa pine stands, postfire logging reduced herbaceous biomass and plant species diversity only during the first 2 years post-burn (Sexton, 1998). In contrast, in stands of California Douglas-fir (*Psuedotsuga menziesii*) that were logged postfire, the effects of reduced shrub and forb biomass persisted from the first year post-burn to 11 years postfire (Stuart et al., 1993). This variation in postfire logging effects points to the importance of pre-burn conditions on postfire vegetation communities (Wright and Bailey, 1982). In the Dogrib burn, logged and burned sites had the highest forage biomass during 2003, almost 40 g/m^2 more herbaceous biomass, with most of the difference caused by forbs.

We suggest the mechanism of reduced forbs in postfire logged areas may be a result of higher and more variable temperatures within postfire logged sites, and competition for space with woody debris left over after postfire operations. Elsewhere, we show a modest temperature difference of +1.1 °C in average daily maximum temperature in postfire logged areas (Hebblewhite et al., 2005, *unpublished report*). Forbs are sensitive to reduced moisture levels, increased temperatures, and drought conditions, which reduce forb development in montane regions (Walker et al., 1995). Thus, unharvested burned trees likely provide important temperature shading (Amaranthus et al., 1989). Postfire logged areas also had higher percent cover of woody debris, and that increased woody debris appeared to reduce forage biomass through competition for space (Hebblewhite et al., 2005, *unpublished report*). Potential mitigation measures for woody debris competition could be similar to site preparation treatments used in clearcutting practices, such as mounding, trenching, etc., such as for conventional clearcutting, which may benefit wildlife species (Nielsen et al., 2004).

While our main objectives were focused on comparing burned and postfire logged areas, our results in the prefire logged sites confirms the importance of pre-burn condition on postfire vegetation response (Wright and Bailey, 1982). Prefire logged sites had the highest forage biomass during 2003, almost 40 g/m^2 more herbaceous biomass, with most of the difference composed of greater forb biomass such as fireweed (*Epilobium* spp.) and *Calamagrostis* spp. (Supplementary Table S2). Regardless of the potential for bottom-up improvements in ungulate forage in postfire logged stands and logged and burned stands, however, elk avoided these stands because of top-down changes in wolf predation risk.

Elk, deer and moose avoided postfire logged stands, measured by both telemetry and pellet counts, and showed higher use and selection for burned and unlogged 'control' sites relative to postfire logged stands. However, in prefire logged stands, pellet counts and telemetry contradicted each other (Tables 1 and 2), telemetry indicating avoidance, pellets, selection by elk for these prefire logged sites. Why the inconsistency? A careful consideration of the scope of inference of the pellet and telemetry studies provides the answer. Telemetry on radiocollared adult female elk from the Ya Ha Tinda elk herd revealed that elk did not use the eastern Dogrib burn (Hebblewhite et al., 2006) where most of the cut and burned treatments occurred (Fig. 1). Thus, it was not avoidance *per se* of the cut and burned treatments, but instead overall avoidance by Ya Ha Tinda elk of the areas in the Dogrib burn which contained the prefire logged treatment. Pellet groups, however, were collected from across the Dogrib burn, and are a reliable measure for inferences applied to the entire burn and other elk herds that used this summer range. Thus, the discrepancy in the prefire logged treatment can be explained in terms of whether we are making inferences about just the Ya Ha Tinda elk herd (who avoided the cut and burned areas) or other elk herds that used the entire Dogrib burn.

Regardless, the question of why did elk (and other ungulates including deer and moose) avoid the postfire logged treatments? The avoidance of postfire logged stands despite higher forage biomass was the result of higher wolf predation risk there. Wolves selected for postfire logged stands because of high forage biomass, matching the distribution of the resources of their main prey, elk, and because they selected roads associated with logging activity. The importance of roads to predator–prey dynamics has long been noted for human hunters (Lyon, 1983) and more recently for wolf–prey dynamics. Wolves in northern Alberta (with low human activity rates) preferred to travel on roads and travel 2.5 times faster on them compared to unroaded forest (James et al., 2004), which may increase predation rates on woodland caribou (*Rangifer tarandus caribou*, McLoughlin et al., 2005). Nearby in the Alberta foothills, Frair et al. (2007) showed elk avoided areas near roads because of increased risks of mortality by both wolves and humans. Thus, interactions between humans, postfire logging, elk and wolves are consistent with a top-down trophic cascade that could translate to impacts on postfire vegetation or other biota in burned and postfire logged areas (Hebblewhite et al., 2005).

The ungulate avoidance of postfire logged areas because of changes to wolf predation risk may also occur in systems where humans are the dominant predator. Dozens of studies over three decades demonstrated that under human predation risk, elk prefer denser cover and avoid roads (Lyon, 1983; McCorquodale, 2000; Rowland et al., 2000; Frair et al., 2007). In the adjacent foothills of Alberta, elk used areas close to forest cover ($\leq$30 m), either in response to predation risk or disturbance from humans, limiting use of large open logged to patch edges (Frair et al., 2007). Because of the large postfire cutblock size, elk selecting to be close to patch edges would avoid large postfire cutblocks, which suggests reduced patch sizes or increased retention may mitigate these negative effects. Thus, roads may be among the most important impact of postfire logging for ungulates because of landscape-scale changes in predation risk in addition to the large impacts of roads

Author's personal copy

on hydrology, invasive species, and other postfire processes (McIver and Starr, 2000; Beschta et al., 2004). In this context then, the novel contribution of our study is to confirm that these same dynamics occur in postfire logging landscapes, confirming the overarching importance of road management associated with postfire logging, much the same as conventional logging.

4.1. Management implications

Any short-term study of a long process such as forest succession following fire suffers from the criticism of too short a sampling frame (Bennett and Adams, 2004). While the first 3 years post-burn is obviously a short period to draw firm conclusions, our research makes a substantial contribution to the literature on postfire logging effects on wildlife by drawing attention to the importance of trophic dynamics. We found limited long-term effects of postfire logging on elk forage by the third year post-burn, in fact, forage biomass may actually be enhanced from an ungulate perspective postfire. Paradoxically, however, we found elk and other ungulates potentially avoided postfire logging because of increased predation risk despite higher forage biomass there, suggesting top-down forces were important in structuring trophic relationships (Hebblewhite et al., 2005). Therefore, managers should consider the interactive effects of predation risk on ungulate habitat in postfire landscapes to evaluate the ecosystem impacts of postfire logging, similar to recommendations of numerous other authors (Beschta et al., 2004; Hutto, 2006; Lindenmayer and Noss, 2006; Schmiegelow et al., 2006). In practice, for trophic dynamics of predator–prey systems, the roads associated with postfire logging may have the greatest negative impacts similar to conventional logging, followed by changes to the ungulate forage resources following postfire logging. While road closures may work to manage human hunters, they will be ineffective for predators like wolves. Therefore, using existing road networks, minimizing the construction of new roads, and carefully managing road removal and restoration following postfire logging will help mitigate the negative effects of postfire logging on terrestrial ecosystems (Lindenmayer and Noss, 2006; Switalski et al., 2004).

Acknowledgements

The following funding agencies provided funding for this research: ACA Challenge Grants in Biodiversity, Foothills Model Forest-Chisholm-Dogrib Fire initiative grants, Parks Canada, Sundre Forest Products LTD., Canon National Parks Science Scholarship for the Americas, and University of Alberta. We thank Rick Smee, Darren Labonte, and James R. Allen, Alberta Sustainable Resource Development (AB-SRD), Tom Daniels and Barry McElhinney from Sundre Forest Products Ltd., Dr. Wayne Strong and Dr. Cormack Gates from University of Calgary, and Cliff White, Ian Pengelly and Darrel Zell from Parks Canada for assistance. We thank the Ya Ha Tinda ranch staff, particularly ranch managers Johnny and Marie Nylund and Rick and Jean Smith for logistical support. Final thanks are reserved for field technicians, in particular Shari Clare, Joe Litke, Mark Lindberg, Cedar Mueller, Judith Wheeler, and Robin Whittington. We thank R. Hutto, D. Dellasala, and D. Lindenmayer for helpful comments on an earlier version of this manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2008.11.009.

References

Amaranthus, M., Jubas, H., David, A., 1989. Stream shading, summer streamflow and maximum water temperature following intense wildfire in headwater streams. In: Berg, N.H. (Ed.), U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. Berkely, CA, pp. 75–78.

Baird, B.N., 2006. Comment on ‘‘Post-Wildfire Logging Hinders Regeneration and Increases Fire Risk’’. Science 313, 5787.

Baker, M.D., Lacki, M.J., 1998. Day-roosting habitat of female long-legged myotis in Ponderosa pine forests. J. Wildl. Manage. 70, 207–215.

Bennett, L.T., Adams, M.A., 2004. Assessment of ecological effects due to forest harvesting: approaches and statistical issues. J. Appl. Ecol. 41, 585–598.

Beschta, R.L., Rhodes, J.J., Kauffman, J.B., Griesswell, R.E., Minshall, G.W., Karr, J.R., Perry, D.A., Hauer, E.R., Frissell, C.A., 2004. Postfire management on forested public lands of the western United States. Conserv. Biol. 18, 957–967.

Blake, J.G., 1982. Influence of fire and logging on non-breeding bird communities of Ponderosa pine forests. J. Wildl. Manage. 46, 404–415.

Boyce M.S., Merrill E.H. 1991. Effects of 1988 fires on ungulates in Yellowstone National Park. Proceedings of the Tall Timbers Fire Ecology Conference 17, 121–32.

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecol. Model. 157, 281–300.

Brodie, J., 2006. An experimentally determined persistence-rate correction factor for scat-based abundance indices. Wildl. Soc. Bull. 34, 1216–1219.

Brown, T.J., Hall, B.L., Westerling, A.L., 2004. The impact of twenty-first century climate change on wildland fire danger in the western United States: an applications perspective. Climatic Change 62, 365–388.

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York.

Dellasala, D.A., Karr, J.K., Schoennagel, T., Perry, D., Noss, R., Lindenmayer, D., Beschta, R., Hutto, R.L., Swanson, M.E., Evans, J., 2006. Post-fire logging debate ignores, many issues. Science 314, 51–52.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2006a. Post-wildfire logging hinders regeneration and increases fire risk. Science 311, 352.

Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2006b. Response to Comments on ‘‘Post-Wildfire Logging Hinders Regeneration and Increases Fire Risk’’. Science 313, 5787.

Fisher, J.T., Wilkinson, L., 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Rev. 35, 51–82.

Frair, J.L., Merrill, E.H., Allen, J.R., Boyce, M.S., 2007. Know thy enemy: experience affects translocation success in risky landscapes. J. Wildl. Manage. 74, 123–140.

Fuller, T.K., 1991. Do pellet counts index white-tailed deer numbers and population change? J. Wildl. Manage. 55, 393–396.

Gessler, P.E., Moore, I.D., McKenzie, N.J., Ryan, P.J., 1995. Soil-landscape modeling and spatial prediction of soil attributes. Int. J. GIS 9, 421–432.

Gillies, C., Hebblewhite, M., Nielsen, S.E., Krawchuk, M., Aldridge, C., Frair, J., Stevens, C., Saher, D.J., Jerde, C., 2006. Application of random effects to the study of resource selection by animals. J. Anim. Ecol. 75, 887–898.

Hebblewhite, M., 2006. Linking forage and predation risk to ungulate population dynamics. Dissertation, University of Alberta, Edmonton, Canada.

Hebblewhite, M., Merrill, E.H., 2007. Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia 152, 377–387.

Hebblewhite, M., Merrill, E.H., 2008. Modeling wildlife–human relationships with mixed-effects habitat selection models. J. Appl. Ecol. 45, 834–844.

Hebblewhite, M., Merrill, E.H., McDermid, G., 2008. A mutli-scale test of the forage maturation hypothesis for a partially migratory montane elk population. Ecol. Monogr. 78 (2), 141–166.

Hebblewhite, M., Merrill, E.H., McDonald, T.E., 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk system. Oikos 111, 101–111.

Hebblewhite, M., Merrill, E.H., Morgantini, L.E., White, C.A., Allen, J.R., Bruns, E., Thurston, L., Hurd, T.E., 2006. Is the migratory behaviour of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. Wildl. Soc. Bull. 34, 1280–1295.

Hebblewhite, M., Percy, M., Merrill, E.H., 2007. Are all GPS collars created equal? Correcting habitat-induced bias using three brands in the Central Can. Rockies. J. Wildl. Manage. 71, 2026–2033.

Hilbe, J., 1999. Zero-inflated Poisson and negative binomial regression. Stata Tech. Bull. 8, 233–236.

Hobson, K.A., Schieck, J., 1999. Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. Ecol. Appl. 9, 849–863.

Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression. John Wiley and Sons, New York.

Hoyt, J.S., Hannon, S.J., 2002. Habitat associations of black-backed and three-toed woodpeckers in the boreal forest of Alberta. Can. J. For. Res. 32, 1881–1888.

Hutto, R.L., 1995. Composition of bird communities following stand-replacement fires in northern rocky-mountain conifer forests. Conserv. Biol. 9, 1041–1058.

Hutto, R.L., 2006. Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. Conserv. Biol. 20 (4), 984–993.

James, A.R.C., Stuart-Smith, A.K., 2000. Distribution of caribou and wolves in relation to linear corridors. J. Wild. Manage. 64 (1), 154–159.

James, A.R.C., Boutin, S., Hebert, D.M., Rippin, A.B., 2004. Spatial separation of caribou from moose and its relation to predation by wolves. J. Wildlife Manage. 68, 799–809.

Author's personal copy

Karr, J.R., Rhodes, J.J., Minshall, G.W., Hauer, F.R., Beschta, R.L., Frissell, C.A., Perry, D.A., 2004. The effects of postfire salvage logging on aquatic ecosystems in the American West. Bioscience 54 (11), 1029–1033.

Key, C.H., Benson, N.C., 2003. Remote sensing measures of fire severity: the normalized burn ratio. In: Rocky Mountain Research Station, GTR, USGS, Glacier, Montana.

Koivula, M., Spence, J.R., 2006. Effects of postfire salvage logging on boreal mixed-wood ground beetle assemblages (*Coleoptera*, *carabidae*). For. Ecol. Manage. 236, 102–112.

Krebs, C.J., 1989. Ecological Methodology. Harper Collings Publishers, New York.

Kunkel, K.E., Pletscher, D.H., 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. Can. J. Zool. 72, 1557–1565.

Lima, S.L., 2002. Putting predators back into behavioral predator–prey interactions. Trends Ecol. Evol. 17, 70–75.

Lindenmayer, D.B., Noss, R.F., 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conserv. Biol. 20, 949–958.

Lindenmayer, D.B., Burton, P.J., Franklin, J.F., 2008. Salvage Logging and its Ecological Consequences. Island Press, New York.

Luttberg, B., Sih, A., 2004. Predator and prey habitat selection games: the effects of how prey balance foraging and predation risk. Israel J. Zool. 50, 233–254.

Lyon, J., 1983. Road density models describing habitat effectiveness for elk. J. For. 22, 592–595.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource Selection by Animals: Statistical Analysis and Design for Field Studies, second ed. Kluwer, Boston, USA.

McCorquodale, S.M., 2000. Habitat ecology and vulnerability to hunting mortality of elk in the southcentral Washington Cascades. Wildlife Biology Program, School of Forestry, University of Montana. Dissertation.

McIver, J.D, Starr, L., 2000. Portland, OR: United States Department of Agriculture—Forest Service; Report nr PNW-GTR-486, 72 pp.

McLoughlin, P.D., Dunford, J.S., Boutin, S., 2005. Relating predation mortality to broad-scale habitat selection. J. Anim. Ecol. 74, 701–707.

Merrill, E.H., Mayland, H.F., Peek, J.M., 1982. Shrub responses after fire in an idaho ponderosa pine community. J. Wild. Manage. 46, 496–502.

Neff, 1968. The pellet-group count technique for big game trend, census, and distribution: a review. J. Wildl. Manage. 32, 597–614.

Nielsen, S.E., Munro, R.H.M., Bainbridge, E.L., Stenhouse, G.B., Boyce, M.S., 2004. Grizzly bears and forestry II. Distribution of grizzly bear foods in clearcuts of west-central Alberta, Canada. For. Ecol. Manage. 199, 67–82.

Noss, R.F., Lindenmayer, D.B., 2006. The ecological effects of salvage logging after natural disturbance—introduction. Conserv. Biol. 20, 946–948.

Peek, J.M., 1974. Initial response of moose to a forest fire in Northeastern Minnesota. Am. Midl. Nat. 91, 435–438.

Phillips, I.D., Cobb, T.P., Spence, J.R., Brigham, R.M., 2006. Salvage logging, edge effects, and carabid beetles: connections to conservation and sustainable forest management. Environ. Entom. 35, 950–957.

Pierce, B.M., Bowyer, R.T., Bleich, V.C., 2004. Habitat selection by mule deer: forage benefits or risk of predation? J. Wild. Manage. 68, 533–541.

Pulliam, H.R., 1989. Individual behaviour and the procurement of essential resources. In: Roughgarden, J., May, R.M., Levin, S.A. (Eds.), Perspectives in Ecology. Princeton University Press, Princeton, USA, pp. 25–38.

Rowland, M.M., Wisdom, M.J., Johnson, B.K., Kie, J.G., 2000. Elk distribution and modeling in relation to roads. J. Wild. Manage. 64, 672–684.

Sachro, L.L., Strong, W.L., Gates, C.C., 2005. Prescribed burning effects on summer elk forage availability in the Subalpine zone, Banff National Park. Environ. Manage. 77, 183–193.

Schmiegelow, F.K.A., Stepnisky, D.P., Stambaugh, C.A., Koivula, M., 2006. Reconciling salvage logging of boreal forests with a natural-disturbance management model. Conserv. Biol. 20, 971–983.

Sexton, T.O., 1998. Ecological effect of post-wildfire management activities (salvage-logging and grass-seeding) on vegetation composition, diversity, biomass, and growth and survival of *Pinus pondersa* and *Purshia tridenta*. Oregon State University. MS thesis.

Skrondal, A., Rabe-Hesketh, S., 2004. Generalized latent variable modeling: multilevel, longitudinal, and structural equation models. Chapman and Hall, New York, NY, USA.

Smith, J.K., 2000. Wildland fire in ecosystems: effects of fire on fauna. Ogden, UT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. Notes: Gen. Tech. Rep. RMRS-GTR-42-vol 1.

Sokal, R.R., Rohlf, F.J., 1995. Biometry. W.H. Freeman and Company, New York.

Stokstad, E., 2006. Academic conduct—University bids to salvage reputation after flap over logging paper. Science 312, 1288.

Stuart, J.D., Grifantini, M.C., Fox, L., 1993. Early successional pathways following wildfire and subsequent silvicultural treatment in Douglas-fir hardwood forests, NW California. For. Sci. 39, 561–572.

Switalski, T.A., Bissonette, J.A., Deluca, T.H., Luce, C.H., Madej, M.A., 2004. Benefits and impacts of road removal. Front. Ecol. Environ. 2, 21–28.

Taper, M.L., Gogan, P.J., 2002. The northern Yellowstone elk: density dependence and climatic conditions. J. Wild. Manage. 66, 106–122.

Turner, M.G., Hargrove, W.W., Gardner, R.H., Romme, W.H., 1994. Effects of fire on landscape heterogeneity in Yellowstone-National-Park, Wyoming. J. Veg. Sci. 5, 731–742.

Walker, M.D., Ingersoll, R.C., Webber, P.J., 1995. Effects of interannual climate variation on phenology and growth of two Alpine Forbs. Ecology 76, 1067–1083.

Wiens, J.A., Parker, K.R., 1995. Analyzing the effects of accidental environmental impacts—approaches and assumptions. Ecol. Appl. 5, 1069–1083.

Wright, H.A., Bailey, A.W., 1982. Fire Ecology. John Wiley and Sons, New York, NY.

Van Dyke, F., Darragh, J.A., 2007. Response of elk to changes in plant production and nutrition following prescribed burning. J. Wild. Manage. 71, 23–29.