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Forest Ecology and Management 199 (2004) 51–65
Forest Ecology and Management
www.elsevier.com/locate/foreco

Grizzly bears and forestry I. Selection of clearcuts by grizzly bears in west-central Alberta, Canada

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Received 7 February 2004; received in revised form 13 April 2004; accepted 13 April 2004

Abstract

We examined if clearcuts were selected as habitats by grizzly bears (*Ursus arctos* L.) in west-central Alberta during three seasons: hypophagia, early hyperphagia, and late hyperphagia. Our objectives were to describe seasonal habitat selection of clearcuts using resource selection functions at two scales. At the first scale, we assessed patch or third-order selection by comparing use (radiotelemetry) with study area-wide random locations and a dummy variable identifying whether locations occurred within or outside of clear-cut boundaries. At the second scale, we assessed within-patch or fourth-order selection by comparing locations (use and random) found within clearcuts and environmental covariates of terrain, silviculture, and landscape metrics. Finally, we examined diurnal versus crepuscular/nocturnal use of clearcuts by comparing the two with an expected 50:50 ratio.

At the third-order scale, grizzly bears used clearcuts with respect to their availability for hypophagia and late hyperphagia, while selecting clearcuts more than expected during early hyperphagia. Fourth-order habitat selection revealed that landscape metrics, silviculture, and terrain were important predictors of grizzly bear use during hypophagia and late hyperphagia, while terrain appeared to be the most important predictor during early hyperphagia. Overall, grizzly bears avoided clear-cut interiors and preferred clearcuts with higher perimeter-to-edge ratios. Clearcuts were significantly more likely to be used during crepuscular/nocturnal periods. Intermediate-aged (~30 years old) clearcuts were selected during hypophagia, whereas recent and old clearcuts were selected during late hyperphagia. Bears tended to avoid clearcuts with Donaren mound preparation, while selecting clearcuts with Bracke or shark-fin barrel dragging. These results suggest that landscape metrics, site preparation history, terrain, and season were important factors determining the use of clearcuts by grizzly bears. Future forest planning should strive to maximize habitat quality by: (1) increasing perimeter-to-edge ratio for clear-cut shapes; (2) using low impact and/or positively associated site preparation treatments like Bracke and shark-fin barrel dragging; and (3) limiting human access to areas predicted as high-quality habitat.

Keywords: Alberta; Grizzly bear; Forestry; Habitat selection; Silviculture

1. Introduction

Industrial resource extraction activities, including forestry, threaten the persistence of grizzly bears (*Ursus arctos* L.) in North America (Banci et al.,

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0378-1127/$ – see front matter
doi:10.1016/j.foreco.2004.04.014

1994; Clark et al., 1996; McLellan, 1998) by fragmenting secure (free of human disturbance) habitats and increasing human access to previously remote landscapes. This is especially evident in the Central Rockies Ecosystem of Canada where unprecedented growth of human population and resource extraction has co-occurred (Schneider et al., 2003). For grizzly bears, increased human access has amplified human-caused mortality, the primary source of death for grizzly bears (McLellan and Shackleton, 1988; Benn and Herrero, 2002; Nielsen et al., 2004a). General habitat selection and assessments of road impacts have been widely studied for grizzly bears (McLellan and Shackleton, 1988; Mace et al., 1996, 1999; McLellan and Hovey, 2001; Gibeau et al., 2002; Wielgus et al., 2002). Although forest planning will largely determine overall habitat quality, configuration, and composition of future grizzly bear habitats in forested landscapes, few of these studies have assessed selection patterns by grizzly bears for different forest activities. With continual industrial resource extraction activities expected, viability of grizzly bear populations within managed forest landscapes is uncertain and in need of study.

High-quality grizzly bear habitats generally are considered roadless areas with a mosaic of early seral-staged forests and natural openings in proximity to secure forest stands providing day beds and hiding cover (Herrero, 1972; Blanchard, 1980; Hamer and Herrero, 1987). Fire suppression, however, threatens open-structured habitats, including those required by grizzly bears. Suppression of fire in western North America over the past half century has led to increased woody encroachment of natural openings and extensive succession of early seral or open structured stands (Payne, 1997). Widespread succession without further disturbance can lead to local population declines in grizzly bears (McLellan and Hovey, 2001). Forest management, through development of early seral stage communities, therefore offers an opportunity for management of grizzly bear habitat and ultimately populations. Previous examinations of habitat use, however, have shown consistent avoidance of regenerating clearcuts suggesting potential loss of habitat (Zager et al., 1983; Waller, 1992; McLellan and Hovey, 2001). Most recently, Wielgus and Vernier (2003) found that grizzly bears used clearcuts as available (neither selected nor avoided). Previous grizzly bear work, however, has focused on mountainous landscapes where open habitats were not limiting and often greater in extent than clearcuts. Few if any studies have examined how selection for regenerating clearcuts occurs in foothill boreal-like environments typical of west-central Alberta where forests predominate and natural openings are rare. Moreover, little has been done to examine specific conditions of clearcut use by grizzly bears with respect to food seasons, time of day, and local site and management history conditions. Instead, most have assumed that clearcuts are homogenous and selection consistent among seasons and times of day. Identifying any site and terrain conditions, silvicultural treatments and clear-cut designs that enhance or reduce grizzly bear habitat is important for determining future forest management and conservation planning, as many of North America's grizzly bear populations reside in areas undergoing forest management.

Here we explore selection of habitats by grizzly bears in the upper foothills of west-central Alberta, a forested landscape that has been intensively managed for nearly 50 years. We test the widely held hypothesis that clearcuts were avoided by grizzly bears by examining 4 years of global positioning system (GPS) radiotelemetry data. In the foothills of west-central Alberta we suspected clearcut selection was occurring, as natural openings were not extensively available. Our specific objectives for this paper were threefold: (1) determine differences in grizzly bear selection of clearcuts (patch or third-order selection) by season; (2) describe selection by season for individual clearcuts (within-patch or fourth-order selection) based on scarification, age, distance-to-edge, perimeter-to-edge ratio, and micro-site terrain characteristics; and finally, (3) examine whether there were any differences in selection of clearcuts during diurnal or crepuscular/nocturnal periods. In a companion paper (Nielsen et al., 2004b), we characterize how critical food resources vary within clearcuts to help interpret habitat use patterns observed herein.

2. Methods

2.1. Study area

A study area was delineated for a 2677 km^2 landscape located in the eastern foothills of the Canadian

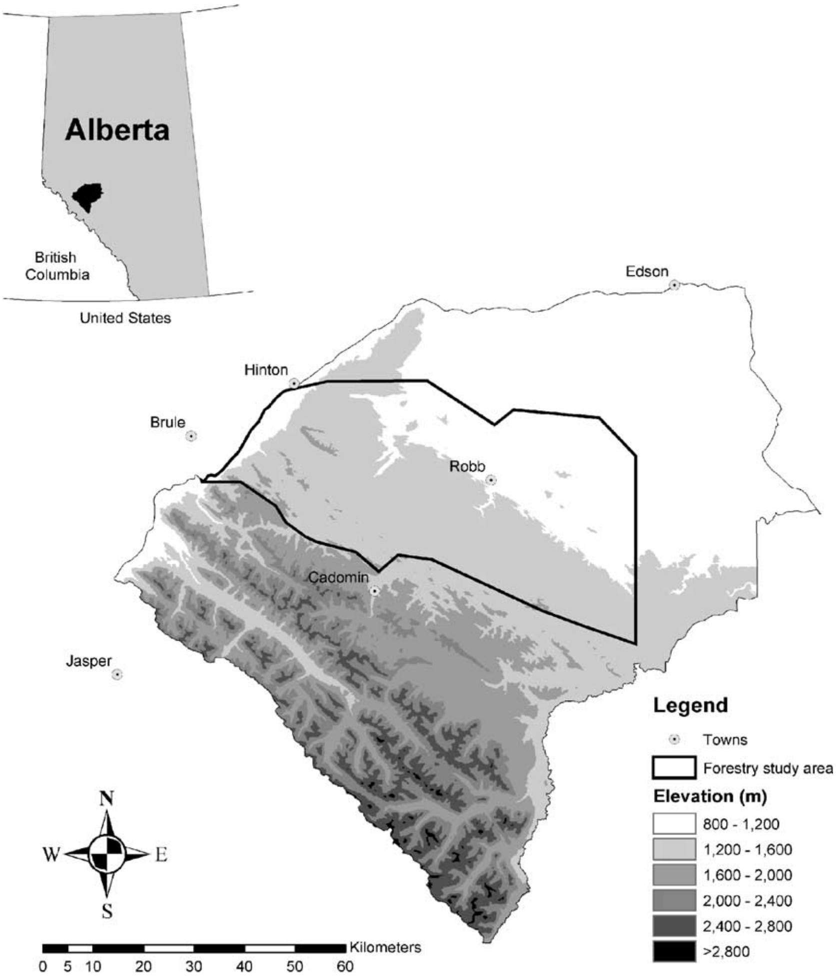

Fig. 1. Study area map depicting elevation, local towns, overall foothills model forest (FMF) study region (map extent), and secondary forestry study area for examining habitat selection related to clear-cut harvesting in west-central Alberta, Canada. Location of FMF study area within Alberta is depicted in the upper left portion of the figure.

Rocky Mountains of west-central Alberta (53°15′N, 117°30′W; Fig. 1). We chose this area because of its long history of forestry and available detailed records of management actions. Within this area, a total of 525 km^2 (19.6% of the area) of forest has been harvested for timber (clearcutting) since 1956 (Fig. 2). Surrounding regenerating clearcuts were closed conifer forests (41.4%), numerous minor forest (e.g., open conifer, deciduous, etc.), and to a lesser extent non-forest (e.g., herbaceous, shrub, etc.) classes (Franklin et al., 2001; Table 1). Closed conifer, the dominant landcover category, was composed of lodgepole pine (*Pinus contorta*), and to a lesser extent three species of spruce (*Picea glauca*, *P. mariana*, and *P. engelmannii*). Minor areas of trembling aspen (*Populus tremuloides*) or balsam poplar (*P. balsamifera*), often mixed with other shrubs including willow (*Salix* spp.), were scattered throughout the area, but most notable in lower elevations or riparian zones. We refer to all landcover and landuse activities occurring outside of clear-cut boundaries as matrix habitat.

Natural sub-region classification based on climate, vegetation, soils, and topography was best described

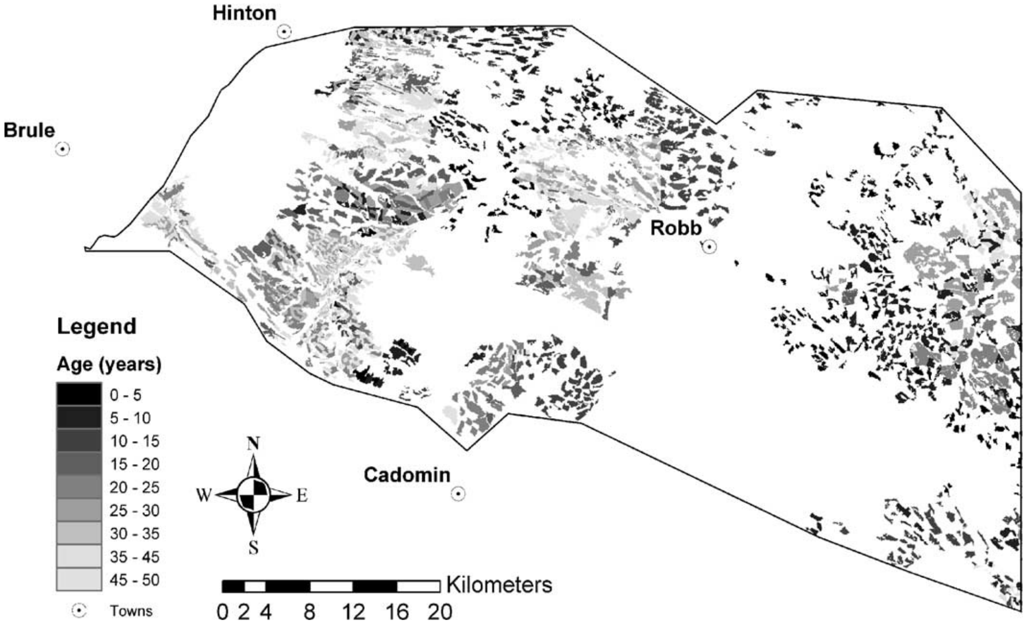

Fig. 2. Mapped clearcuts by 5-year age class in the upper foothills of west-central Alberta, Canada.

Table 1
Area (km^2) and percent composition of land cover classes within the 2677 km^2 study area near Hinton, Alberta

Land cover class	Area (km^2)	Percent
Closed conifer	1109.2	41.4
Clearcut	525.2	19.6
Mixed forest	401.2	15.0
Wetland-open bog	184.0	6.9
Closed deciduous	117.9	4.4
Wetland-treed bog	94.9	3.5
Road/rail/pipeline/well site	76.9	2.9
Non-vegetated	34.4	1.3
Open conifer	31.5	1.2
Shrub	31.2	1.2
Other anthropogenic	26.6	1.0
Herbaceous	17.6	0.7
Water	15.4	0.6
Burn	7.8	0.3
Open deciduous	3.0	0.1
Alpine/subalpine	0.2	0.01
Total	2677.0	100.0

Land cover classes were determined from a remote sensing classification (Franklin et al., 2001) and forestry GIS data on clearcuts.

as upper foothills (Achuff, 1994), with elevations varying from 953 and 1975 m in rolling low mountainous terrain. Summer and winter temperatures averaged 11.5 and −6.0 °C, respectively, with a normal annual precipitation of 538 mm (Beckingham et al., 1996). Prior to 1950, periodic stand-replacing fires were the primary disturbance, averaging 20% of the landscape burned per 20-year period yielding a 100-year fire cycle (Andison, 1998). Since the 1950s, however, there has been a reduction in fires to the region being associated with the initiation of industrial forestry and fire suppression (Tande, 1979; Andison, 1998; Rhemtulla, 1999). Although some stands in remote regions are in advanced stages of succession due to fire suppression, large areas have or continue to be harvested providing the only major mechanism of disturbance. As most grizzly bear foraging in the front slopes of the Canadian Rockies occurs in open forests or meadows (Hamer and Herrero, 1987), clearcuts within heavily forested regions, such as the foothills of west-central Alberta, provide an opportunity or alternative source of food normally only associated with young fire-regenerating stands (Nielsen et al., 2004b).

2.2. Grizzly bear location data

From 1999 to 2002, we captured and collared 8 (5 female, 3 male) sub-adult (2–4 years of age) and 13 (7 female, 6 male) adult (≥5 years of age) grizzly bears from areas within or surrounding the forestry study area using standard aerial darting and leg snaring techniques (Cattet et al., 2003). Bears were fitted with either a Televilt GPS-Simplex or an ATS (Advanced Telemetry Systems) GPS radiocollar. Radiocollars were programmed to acquire locations at intervals of every 4 h, excluding a few collars that were programmed to take a fix every 1 h. Following retrieval of GPS collars and/or remote uploading of collars, grizzly bear locations were imported into a geographic information system (GIS) and used to delineate 100% minimum-convex-polygon (MCP) home ranges (Samuel and Fuller, 1994). These home ranges were used to identify "available" locations for each individual using a random-point generator in ArcView 3.2. Sampling intensities for available locations within MCP home ranges were standardized to 5 points/km^2. For selection analyses on the broader landscape (clearcut versus matrix habitats), all locations falling within the defined study area were used, while selection within clearcuts was examined using only those locations falling within clear-cut boundaries.

To account for variation in habitat use through time (Schooley, 1994; Nielsen et al., 2003), we stratified grizzly bear location data into three seasons based on food habits and selection patterns for the region (Hamer and Herrero, 1987; Hamer et al., 1991; Nielsen et al., 2003). The first season, hypophagia, was defined as den emergence (typically in April) to 14 June. During this season, bears fed on roots of *Hedysarum* spp. and in some instances on carrion. The second season, early hyperphagia, was defined as 15 June to 7 August. During this season, bears fed on ants (myrmecophagy), in some instances ungulate calves, and frequently on green herbaceous material including *Heracleum lanatum*, graminoids, sedges, and *Equisetum arvense*. The third season, late hyperphagia, was defined as 8 August to denning. During this season, bears sought out berries from *Shepherdia canadensis* and *Vaccinium* spp. followed by late season digging for *Hedysarum* spp. Resource selection functions (RSFs) were developed for both clearcut selection and within-clearcut selection using these three seasons. We did not explore year-to-year variation in habitat selection as sample sizes precluded seasonal and yearly stratification of data.

Given that grizzly bears have shown avoidance of non-secure (areas of human activity) areas during diurnal periods (Gibeau et al., 2002), we further assessed whether selection of clearcuts occurred more than expected during crepuscular and nocturnal periods. Diurnal hours were defined as the period occurring between 07:00 and 19:00 h, while crepuscular and nocturnal hours were defined as occurring between 19:00 and 07:00 h. Our definitions of diurnal and crepuscular/nocturnal periods were general only and did not account for changes in sunrise or sunset. To ensure that acquisition rates for these periods were not biased for the global data set, we assessed the proportion of locations acquired during each period using 2×2 contingency χ^2 test and an expected 50:50 ratio.

2.3. Patch-level selection of clearcuts (third-order scale)

We compared seasonal GPS radiotelemetry locations with random or available locations to assess habitat selection for clearcut (1) and matrix habitats (0). Analyses were evaluated at the third-order (patch) scale (Johnson, 1980) following a 'design III' approach, where the individual identity of the animal was maintained for use and available samples (Thomas and Taylor, 1990). For each season, we calculated a resource selection function at the level of the population using the following model structure from Manly et al. (2002):

$$w(x) = \exp(\beta x) \tag{1}$$

where $w(x)$ is the resource selection function (relative probability of occurrence) and β the selection coefficient for the dummy variable x used to indicate whether locations (use or available) were within (1) or outside (0) of clearcut polygons. Logistic regression was used to estimate β in the program Stata (2001). We specified the robust cluster option to calculate our variance around the estimated coefficient using the Huber-White sandwich estimator (White, 1980; Nielsen et al., 2002). Sandwich estimators assumed that observations were independent across clusters, but not necessarily independent within clusters (Long and Freese, 2003). Bear was specified as the cluster,

Table 2
Explanatory map variables used for assessing grizzly bear habitat selection of clearcuts in the upper foothills of west-central Alberta, Canada

Variable code	Description	Type	Range
Age	Age of clearcut (years)	Linear	0–46
Area	Area (km^2) of clearcut	Linear	0.003–2.683
Area:perim	Area (km^2)-to-perimeter (km) ratio	Linear	0.009–2.885
CTI	Compound topographic (wetness) index	Linear	7.34–24.45
Distedge	Distance-to-edge of clearcut (km)	Linear	0–0.8465
Elev	Elevation of location (km)	Linear	974–1712
ScarYN	Scarified clear-cut	Categorical	Yes or No
Scartype	Scarification method	Categorical	10 categories
Solar	Direct solar radiation (WH/m^2) on day 172	Linear	2391–4380

thereby matching the design III approach of the analysis (unit of replication) and avoiding autocorrelation and/or pseudoreplication of locations within individual bears. We further corrected for habitat- and terrain-induced GPS-collar bias (Obbard et al., 1998; Dussault et al., 1999; Johnson et al., 2002) by using probability sample weights for grizzly bear locations (Frair et al., 2004). Probability sample weights were based on local models predicting GPS fix acquisition as a function of terrain and landcover characteristics (Frair et al., 2004). For the clearcut selection model we report results as an odds ratio based on the exponentiated form of β. Reported odds ratios were interpreted as the likelihood that grizzly bears were using clearcuts compared with matrix habitats for a particular season. Use of clearcuts by grizzly bears in concordance with availability would therefore be represented as 1.0, while selection would be >1.0 and avoidance <1.0. Finally, we tested whether GPS radiotelemetry data associated with clearcut use occurred more in diurnal or crepuscular/nocturnal periods by using a 2×2 contingency χ^2 test and an expected 50:50 ratio.

2.4. Within-patch selection of clearcuts (fourth-order scale)

For analyses of selection within clearcuts, we selected all locations occurring within clearcut polygons and divided our observations into two groups following a random sample test set validation. The first group, the model-training group, represented a random 85% subsample used for model development, while the remaining sub-sample (15%), the model-testing group, was used for assessing model performance by independent validation. Given that observations were within-clearcut patches, our analytical design followed a fourth-order scale of habitat selection (Johnson, 1980). Individual identity of animals (design III; Thomas and Taylor, 1990) was also maintained. Using model-training data and explanatory map variables (Table 2) for each season we developed RSF models by assuming the following structure from Manly et al. (2002):

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_k x_k)$$

where $w(x)$ is the resource selection function for a vector of predictor variables, x_i, and β_i values are the corresponding selection coefficients. Logistic regression was used to estimate selection coefficients in Stata (2001). Linear predictor variables (Table 2) were assessed for collinearity through Pearson's correlations (r) and variance inflator function (VIF) diagnostics. All variables with correlations $r > |0.6|$, individual VIF scores >10, or the mean of all VIF scores considerably larger than 1 (Chatterjee et al., 2000) were assumed to be collinear. Area of clearcut and area-to-perimeter ratio were the only correlated ($r = 0.68$) variables, and thus were not considered together for inclusion in the same model. No further evidence of collinearity was evident using VIF tests. Using independent explanatory map variables, we generated five a priori candidate models (Table 3). Each candidate model corresponded to a set of similar variables or combination of variables that we hypothesized as being important for grizzly bears. We evaluated model selection for the five candidate models using Akaike's information criteria (AIC; Burnham and Anderson, 1998; Anderson et al., 2000). Akaike weights (w_i) were used to determine the approximate 'best' model given the data and candidate models tested. Methods for controlling autocorrelation and

Table 3
A priori seasonal candidate models used to describe habitat selection within clearcuts by grizzly bear in the upper foothills of west-central Alberta, Canada

Model no.	Model name	Model structure
1	Scarification model	Age + age^2 + scarYN + area
2	Silviculture model	Age + age^2 + scartype + area
3	Terrain model	CTI + CTI^2 + elev +$elev^2$ + solar
4	Landscape model	Distedge + area:perim
5	Comprehensive model	Age + age^2 + CTI + CTI^2 + solar + scartype + distedge + area:perim

Model number, name, and structure are provided.

GPS radiotelemetry bias, explained in the previous section, were similarly used here.

Using testing data, we assessed the predictive performance of models by comparing map predictions with frequency of within-sample independent testing data (grizzly bear use locations) in specified bins (Boyce et al., 2002). A total of 10 quantile bins were generated based on the distribution of predicted habitats in the study area from the AIC-selected seasonal model. These bins ranked from habitats with low relative probability of occurrence (1) to habitats with high relative probably of occurrence (10). Models that performed well were characterized by having successively more model-testing GPS radiotelemetry locations in higher value habitat bins, while poor habitat bins contained few animal locations. We used a Spearman rank correlation (r_s) to assess the relationship among number of observed grizzly bear model-testing locations per bin and bin rank (Boyce et al., 2002). We considered a model to be predictive if r_s was positive and significant.

2.4.1. Site-specific predictor variables

Age of clearcut, in years, for each radiotelemetry and available location was determined from a GIS forestry polygon database provided by Weldwood of Canada Ltd. (Hinton, Alberta). Size of clearcut, in km^2, was also used as a predictor to assess whether small clearcuts were more attractive to grizzly bears from a security or ecotone basis. To determine clearcut size, we maintained all original clearcut boundaries. Finally, silviculture and/or site preparation data were joined with GIS harvest polygons and stratified into nine separate treatments and a control (no treatment) to test for local clearcut site history effects (Table 4).

We assessed the influence of two landscape metrics on grizzly bear habitat selection. These metrics were distance-to-clearcut edge (km) and area (km^2)-to-perimeter (km) ratio. A 10 m grid was used to determine distance-to-edge (matrix habitat) using the straight-line distance function in the Spatial Analyst extension of ArcGIS 8.1. The area-to-perimeter ratio was calculated for each polygon based on the estimated clearcut size and perimeter from a GIS.

To assess how terrain and local site conditions influenced the pattern of habitat selection for grizzly bears, we used a 26.7 m digital elevation model (DEM). From the DEM, we estimated elevation (km) for each use or available location. We further derived two terrain-related variables from the same DEM. First, we estimated an index of soil wetness commonly referred to as the compound topographic index (CTI), previously found to correlate with several soil attributes including horizon depth, silt percentage, organic matter, and phosphorous (Moore et al., 1993; Gessler et al., 1995). A CTI grid was calculated using the spatial analyst extension in ArcView 3.2 and a CTI script from Rho (2002). Second, we used the DEM to

Table 4
Mechanical silviculture and site preparation treatments assessed for grizzly bear habitat selection

Scarification type	Description
BLAD	Blade (modified)
BRAC	Bracke
DONM	Donaren mound
DRAG	Drag (light or heavy)
DRSF	Drag shark fin barrels
DSTR	Disc trencher
EXCA	Excavator mound
OTHR	Other method (hand and unknown)
PLOW	Plough (Crossley, C&H, C&S ripper)
NONE	Control (no silvicultural site preparation recorded)

derive total potential direct incoming solar radiation (WH/m^2) for summer solstice (day 172) using the Solar Analyst 1.0 extension in ArcView 3.2.

3. Results

3.1. Patch-level selection of clearcuts (third-order scale)

A total of 10,127 locations from 21 grizzly bears were recovered from the identified study area. Of these, 2381 or 23.5% of locations were located within clear-cut polygons. The selection of clearcuts compared with all other landcover categories (matrix) varied by season (Table 5). During hypophagia, grizzly bears selected clear-cut habitats close to that which was expected based on availability. The estimated odds ratio for clearcut selection was 1.14 (95% CI = 0.88 to 1.46) times that of the landscape matrix. In contrast, for early hyperphagia, we found higher rates of clearcut selection. During this season, clearcuts were significantly selected over that of matrix habitats with an odds ratio of 1.56 (CI = 1.31, 1.85). Bears were therefore on average more than one and a half times more likely to select clearcuts over matrix habitats. Finally, during late hyperphagia, grizzly bears once again selected clearcut habitats close to that which would be expected based on habitat availability, although slightly less than matrix habitats with an estimated odds ratio of 0.85 (CI = 0.59, 1.23). Fine-scale temporal patterns of clearcut use differed for diurnal and crepuscular/nocturnal periods. Clearcuts were used more than expected during crepuscular/nocturnal periods ($\chi^2 = 5.69$, 1 d.f., $P = 0.017$). No evidence of bias in diurnal versus crepuscular/nocturnal acquisitions in animal locations was evident for the global data set ($\chi^2 = 1.25$, 1 d.f., $P = 0.264$), suggesting that the selection of clearcuts for the crepuscular/nocturnal period was a biological effect.

3.2. Within-patch selection of clearcuts (fourth-order scale)

3.2.1. Hypophagia

A total of 734 GPS radiotelemetry locations from 14 grizzly bears were acquired from clearcuts during hypophagia. Of the five a priori models assessed for the season, the comprehensive model showed the greatest AIC support (Table 6). During this period, grizzly bears selected intermediate-aged (~30 years) clearcuts (Fig. 4) that were more complex in shape (negative area-to-perimeter ratio), while animal locations were consistently closer to clear-cut edges than random locations (Table 7). There did not appear to be any relationship among grizzly bear location and the compound topographic index (CTI) of soil wetness, although the terrain variable of potential direct incoming solar radiation did appear to be important. Grizzly bears selected for areas of low solar radiation during this season. Lastly, silvicultural treatments were selected within the final model. Responses of site preparation treatments compared to control sites without any treatment varied from positive to negative. In general, bears selected for clearcuts that were scarified with Bracke, dragging, shark-fin barrel dragging, disc-trenching, excavator, and plow treatments, although only shark-fin barrel dragging had a strong consistent effect (Fig. 3; Table 7). In contrast, bears tended to avoid (compared with controls) blade and Donaren mound clearcuts, although neither treatment was overly different from that of controls (Table 7). For between treatment effects, only plow (selection) and Donaren mound (avoidance) treatments were near to being different from one another when comparing 95% confidence intervals. Predictive accuracy

Table 5
Seasonal estimates of habitat selection for clear-cuts (1) by grizzly bears compared to matrix habitats (0; reference category) in the upper foothills of west-central Alberta, Canada

Season	Coefficient	Robust (S.E.)	95% CI		Odds ratio	95% CI	
			Lower	Upper		Lower	Upper
Hypophagia	0.128	0.128	−0.124	0.379	1.137	0.883	1.461
Early hyperphagia	0.443	0.088	0.270	0.616	1.557	1.310	1.852
Late hyperphagia	−0.162	0.189	−0.531	0.208	0.850	0.588	1.231

Table 6
AIC-selected models for hypophagia, early hyperphagia, and late hyperphagia periods

Season and candidate model	K_i	−2LL	AIC	Δ_i	w_i
Hypophagia					
Scarification model	5	5947.4	5957.4	103.1	<0.001
Silviculture model	13	5914.9	5940.9	86.6	<0.001
Site model	5	6013.8	6023.8	169.5	<0.001
Landscape model	3	6023.1	6029.1	174.8	<0.001
Comprehensive model	17	5820.3	5854.3	0.0	1.0
Early hyperphagia					
Scarification model	5	7634.7	7644.7	180.2	<0.001
Silviculture model	13	7575.7	7601.7	137.2	<0.001
Site model	5	7454.5	7464.5	0.0	1.0
Landscape model	3	7641.2	7647.2	182.7	<0.001
Comprehensive model	17	7522.0	7556.0	91.5	<0.001
Late hyperphagia					
Scarification model	5	4914.1	4924.1	163.5	<0.001
Silviculture model	13	4830.2	4856.2	95.6	<0.001
Site model	5	4938.0	4948.0	187.4	<0.001
Landscape model	3	4906.3	4912.3	151.7	<0.001
Comprehensive model	17	4726.6	4760.6	0.0	1.0

Number of parameters (K_i), model −2 log likelihood (−2LL), AIC, change in AIC (Δ_i) from lowest model, and Akaike weights (w_i) of model support are reported.

Table 7
Estimated seasonal AIC-selected model coefficients

Variable code	Hypophagia		Early hyperphagia		Late hyperphagia	
	Coefficient	S.E.	Coefficient	S.E.	Coefficient	S.E.
Age	0.098	0.027	–	–	−0.081	0.061
Age^{2}[a]	−0.145	0.059	–	–	0.207	0.114
CTI	−0.172	0.225	−0.108	0.105	0.157	0.169
CTI^2	0.694	0.930	0.762	0.430	0.029	0.629
Elev	–	–	0.025	0.016	–	–
Elev^{2}[a]	–	–	−0.079	0.058	–	–
Solar[a]	−1.164	0.321	0.889	0.298	−0.170	0.791
Scartype						
BLAD	−0.268	0.292	–	–	−0.300	0.866
BRAC	0.593	0.417	–	–	0.407	0.857
DONM	−1.745	1.239	–	–	−0.711	1.050
DRAG	0.387	0.501	–	–	−0.358	1.084
DRSF	0.783	0.365	–	–	0.205	0.934
DSTR	0.166	0.476	–	–	−0.273	0.649
EXCA	0.089	0.701	–	–	−0.658	1.200
PLOW	0.470	0.245	–	–	−0.343	0.842
Distedge	−2.253	1.038	–	–	−3.518	0.643
Area:perim	−4.850	1.805	–	–	−5.816	3.808

Due to perfect avoidance relating to low sample sizes for the scarification treatment (scartype) 'OTHR', this category was not estimated.
[a] Coefficients for elev^2 and solar are reported at 1000 times their value, while age^2 and CTI^2 are 100 times their actual value.

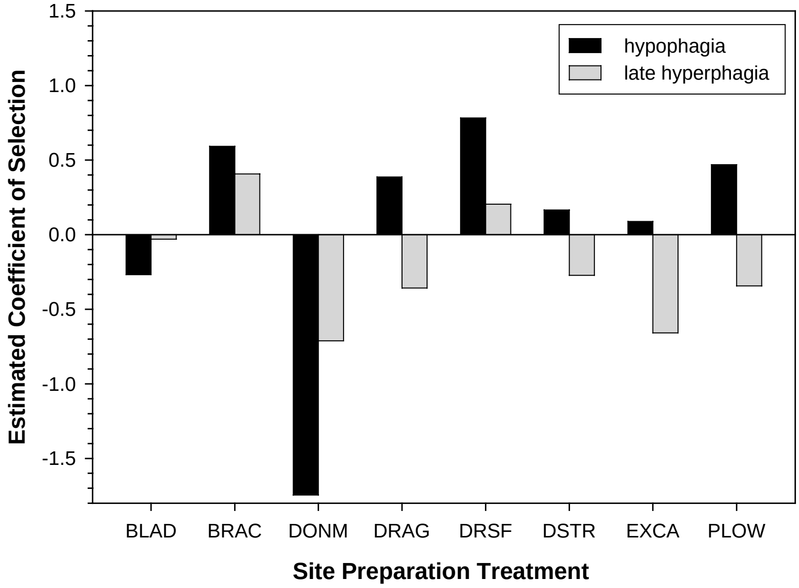

Fig. 3. Estimated silvicultural coefficients for hypophagia and late hyperphagia seasons based on AIC-selected models and contrasts with no treatment (reference category). Category 'other' was withheld due to limitations in estimation caused by perfect collinearity from too few locations. Refer to Table 3 for description of treatment codes.

of the AIC-selected hypophagia model using withheld model-testing data was good with a significant positive Spearman rank correlation ($r_s = 0.915$, $P < 0.001$), suggesting potential utility in using hypophagia clear-cut habitat maps for conservation.

3.2.2. Early hyperphagia

A total of 1005 GPS radiotelemetry locations from 15 grizzly bears were acquired from clearcuts during the early hyperphagia period. Of the five a priori models assessed, the terrain model showed the greatest AIC support (Table 6). During this period, areas with high levels of direct incoming solar radiation were best associated with animal locations, while elevation and soil wetness (CTI) were only weakly related to bear locations (Table 7). Predictive accuracy of the AIC-selected early hyperphagia model using model-testing data was good with a significant positive Spearman rank correlation ($r_s = 0.964$, $P < 0.001$), again suggesting potential utility in mapping seasonal clearcut habitat.

3.2.3. Late hyperphagia

A total of 642 GPS radiotelemetry locations from nine grizzly bears were acquired from clearcuts during the late hyperphagia period. Of the five a priori models assessed, the comprehensive model showed the greatest AIC support (Table 6). During this period, coefficients for direct potential incoming solar radiation and soil wetness (CTI) largely overlapped (95% CI) 0 suggesting a weak relationship, while age of clearcut and perimeter-to-edge ratio, although partially overlapping 0, were influential (Table 7). Grizzly bears tended to use clearcuts that were irregular in shape and either young or more preferably old (up to 46 years; Fig. 4). Like that of hypophagia, distance-to-edge of clearcut was strongly negative (i.e., increasing distance from edge corresponded to decreasing levels of use) suggesting hiding cover or ecotone relationships. Finally, silvicultural treatments again appeared in the AIC-selected model. Bears tended to select for areas that were scarified with Bracke and shark-fin barrel dragging, although confidence intervals were large and overlapping zero (Fig. 3; Table 7). Avoidance of Donaren mound, dragging, disc-trencher, excavator, and plow treatments were suggested, but again noisy. No differences were evident between silvicultural treatments. Predictive accuracy of the AIC-selected late hyperphagia model using model-testing data was good with a significant positive Spearman

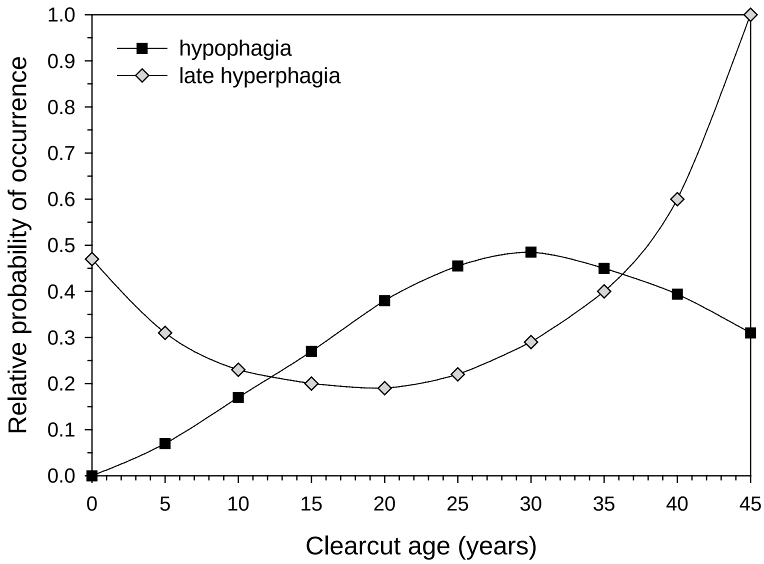

Fig. 4. Relative probability of grizzly bear occurrence within west-central Alberta clearcuts as a function of clearcut age and season. All remaining covariates were held at their mean level. Only seasons that included of clearcut age within AIC-selected models were depicted.

rank correlation ($r_s = 0.770$, $P = 0.009$), suggesting potential utility in mapping seasonal clear-cut habitat. The predictive relationship, however, was less significant than the previous two seasons warranting greater caution in use.

4. Discussion

We reject the hypothesis that grizzly bears avoid clearcuts. We found that grizzly bears selected clearcuts during early hyperphagia, while we could not show a statistical avoidance or selection of clearcuts during hypophagia (non-significant trend of clearcut selection) and late hyperphagia (non-significant trend of clear-cut avoidance). Except for a recent study by Wielgus and Vernier (2003), this seasonal selection of clearcuts (according to availability) contradicts previous examinations of habitat selection by grizzly bears (Zager et al., 1983; Waller, 1992; McLellan and Hovey, 2001). However, most previous work has occurred in mountainous terrain where natural openings (e.g., alpine meadows) and/or large naturally regenerating forests (burns) were available to bears. We suggest that the general lack of large natural openings in our foothill landscape made clearcuts an attractive alternate habitat. Ultimately, the availability of early seral-staged forests or natural openings may explain whether grizzly bears will use clearcuts, as grizzly bears are known to prefer mosaic areas of forest and non-forest habitat (Herrero, 1972). Where fire suppression and succession has led to little if any forest openings, grizzly bears have adapted by utilizing closely related anthropogenic sites, such as clearcuts. Long-term grizzly bear research in Yellowstone has shown a general flexibility or adaptive nature to grizzly bear foraging, maximizing their nutrition through learned behavior (Craighead et al., 1995). Nielsen et al. (2004b) found the occurrence of critical grizzly bear foods, including roots and tubers, herbaceous materials, and ants, to be more common in clearcuts than surrounding forests. Grizzly bears in the foothills of west-central Alberta may have adapted, like that of Yellowstone bears, to changes in landscape composition and associated food resources. Although clearcuts provided a possible resource surrogate for natural openings and young fire-regenerated forests, the associated risk of human-caused mortality due to increased human access may offset this benefit (Nielsen et al., 2004a).

Grizzly bears not only used clearcuts differentially according to season, but also according to time of day.

Overall, there was a trend for grizzly bear use of clearcuts during crepuscular/nocturnal periods, rather than diurnal hours. Although our definitions of diurnal and crepuscular/nocturnal periods did not follow actual sunrise and sunset patterns, our results do point to differences in fine temporal scales, suggesting that activity (bedding versus foraging) and perhaps local security may be important. Previous work on habitat selection for grizzly bears in neighboring Banff National Park support changes in habitat selection between diurnal and nocturnal periods. Gibeau et al. (2002) found that selection of high-quality habitats near areas of human activity were greatest during the nocturnal period when security was highest. Alternatively, use of clearcuts at night may simply reflect thermal demands, especially in mid-to-late summer when high daytime temperatures may force animals to bed in forest stands, with foraging in clearcuts and other open areas restricted to the cooler crepuscular and nocturnal periods. Regardless of the mechanism, short-term (daily) temporal variation in habitat use of clearcuts was observed suggesting that further research into the subject is needed. This is especially relevant as most historic grizzly bear habitat assessments have used VHF radiotelemetry data that was largely collected during diurnal periods, perhaps helping further explain the disparity between our results (seasonal selection of clearcuts) and other studies (avoidance of clearcuts).

Site-specific (within-patch) habitat selection models proved predictive for each season, suggesting that terrain, silviculture, and landscape metrics were important determinants of local clearcut use. Clearcuts cannot therefore be considered uniform in habitat quality, as is usually the case for most grizzly bear habitat work. Small-scale differences in terrain, silviculture, and landscape metrics within or between clearcuts can result in major differences in predicted animal occurrence. Changes, however, were not consistent between seasons as bears were presumably responding to spatio-temporal fluctuations in the availability of critical food resources that individually responded to local environmental gradients and site history characteristics (Nielsen et al., 2004b). Researchers examining grizzly bear habitats should consider introducing environmental covariates that describe age, landscape metrics, silviculture, and terrain.

Landscape metric variables, distance-to-edge and edge-to-perimeter ratio were consistent predictors of grizzly bear use for both the hypophagia and late hyperphagia periods. Grizzly bears occurred nearer to clear-cut edges, while also selecting for clearcuts that were more irregular in shape. These landscape factors, taken together with the observed crepuscular/nocturnal use of clearcuts, help support the hypothesis that hiding cover and/or local security-related issues are important considerations in habitat selection by grizzly bears (Gibeau et al., 2002).

Silvicultural effects on habitat selection for the hypophagia and late hyperphagia seasons varied from negative to positive. Bracke and shark-fin barrel dragging were selected over that of control treatments (no silviculture) for both seasons, but only shark-fin barrel dragging for the hypophagia season had a strong positive effect. In comparison, clearcuts with Donaren mound or blade site preparation were avoided for each season, although confidence intervals were too variable to be certain of this effect. For between-treatment comparisons, Donaren mound (avoidance) and plow (selection) treatments in the hypophagia season were noteworthy of a difference. Grizzly bear use of clearcuts based on silvicultural treatment likely reflected differences in available food resources, as Nielsen et al. (2004b) observed both negative (*Hedysarum* spp. and *S. canadensis*) and positive (*Equisetum* spp.) changes in food occurrence with mechanical scarification.

Age of clearcut was also an important predictor of grizzly bear use. Intermediate-aged (~30 years) clearcuts were most frequently selected during hypophagia, while recent and old (up to 46 years) clearcuts were selected more than intermediate-aged clearcuts during late hyperphagia. The use of intermediate-aged sites during hypophagia most likely reflected distribution of *Hedysarum* spp., as bears readily seek out roots from *Hedysarum* during this season (Hamer and Herrero, 1987; Hamer et al., 1991). Further, Nielsen et al. (2004b) found *Hedysarum* occurrence to be greatest in clearcuts with approximately 25% canopy cover. As canopy cover was correlated with clearcut age ($r = 0.66$), sites with more *Hedysarum* were likely to also be intermediate in age. In comparison, selection of recent and old clearcuts during late hyperphagia likely reflected late season foraging for fruit-bearing species such as *S. canadensis* in old clearcuts and *Rubus idaeus* and herbaceous foods in young clearcuts.

Finally, micro-site terrain features were more important predictors of bear use than landscape metrics or silviculture during early hyperphagia. Grizzly bears selected for areas with high incoming direct solar radiation, which supports myrmecophagy activities (Elgmork and Unander, 1999; Swenson et al., 1999). Ants, typically foraged during early hyperphagia (Hamer and Herrero, 1987; Hamer et al., 1991), tend to be associated with dry, warm slopes (Crist and Williams, 1999; Nielsen et al., 2004b) and occur with greater abundance in clearcuts than unharvested forests (Knight, 1999; Nielsen et al., 2004b). We did not find a strong relationship between grizzly bear use of clearcuts and the soil wetness index, despite the importance of the variable for describing the occurrence of a number of critical grizzly bear foods (Nielsen et al., 2004b).

Habitat selection models for the three examined seasons were predictive based on assessments of independently withheld data suggesting utility in habitat mapping for management and conservation purposes. Such maps could describe both fine-scale differences in habitat quality within clearcuts and coarse-scale differences between clearcuts. Managers could use resulting habitat maps to identify on-the-ground conservation actions, such as determining which roads are in need of deactivation or seasonal closure. Without restricting human access to identified high-quality habitats, risk of mortality will increase, as humans and bears will be placed in close proximity to one another (Mattson et al., 1996a; Nielsen et al., 2004a).

5. Conclusion

Grizzly bears selected clearcuts in the foothills of west-central Alberta. Selection, however, occurred differentially depending on micro-site terrain, landscape metrics, silvicultural history, and season. Management or even enhancement of grizzly bear habitat through forest management appears feasible, especially for areas that lack extensive natural openings or recent fires. We suggest that future forest planning strive to maximize grizzly bear habitat by: (1) increasing perimeter-to-edge ratio for clear-cut shapes; (2) using low impact and/or positively associated site preparation treatments like Bracke and shark-fin barrel dragging; and (3) limiting human access to areas predicted as high-quality habitat. Use of prescribed fire, as a silvicultural treatment, should also be considered along with establishment of food plots for negatively impacted grizzly bear foods (Nielsen et al., 2004b). Limiting human access to high-quality sites helps address population-level factors. In particular, risk of human-caused mortality increases significantly for areas with open public roads (Benn and Herrero, 2002; Nielsen et al., 2004a; Johnson et al., in press). Without addressing habitat occupancy and mortality concurrently, attractive sink conditions may develop where animals are drawn to locations where survival is low (Knight et al., 1988; Delibes et al., 2001). Public education programs targeted at reducing illegal mortalities have been successful elsewhere (Schirokauer and Boyce, 1998) and should also be considered. Finally, long-term forest management will likely modify habitat use by grizzly bears, as the proportion of harvested to non-harvested habitats change. Future research should consider how grizzly bear habitat use changes as the landscape-level context of forest harvesting changes.

Acknowledgements

We thank the Challenge Grants in Biodiversity Program (supported by the Alberta Conservation Association) for research funding in the field. The Department of Biological Sciences at the University of Alberta and the FS Chia Ph.D. Scholarship provided support for the senior author. Overall funding support for the Foothills Model Forest Grizzly Bear Project was provided by Ainsworth Lumber, Alberta Conservation Association (ACA), Alberta Energy Company, Alberta Sustainable Resource Development, Alberta Newsprint, Anderson Resource Ltd., AVID Canada, BC Oil and Gas Commission Environmental Fund, Blue Ridge Lumber (1981 Ltd.), BP Canada Energy Company, Burlington Resources, Canada Centre for Remote Sensing, Canada Resources Ltd., Canadian Forest Products, Canadian Hunter, Canadian Wildlife Service, Cardinal River Coals Ltd., Foothills Model Forest, GeoAnalytic Ltd., Gregg River Resources, Inland Cement, Luscar Sterco (1977) Ltd., Millar

Western Pulp Ltd., Mountain Equipment Coop, Natural Science and Engineering Research Council (NSERC) of Canada, Parks Canada, Petro-Canada, Petroleum Technology Alliance of Canada (PTAC), Rocky Mountain Elk Foundation, Suncor, Sundance Forest Industries, Sunpine Forest Products Ltd., Telemetry Solutions, The Center for Wildlife Conservation (USA), Trans Canada Pipeline, University of Alberta, University of Calgary, University of Saskatchewan, University of Washington, Weldwood of Canada Ltd., Western College of Veterinary Medicine, Weyerhaeuser of Canada Ltd., and World Wildlife Fund. We thank J. Duval, C. Popplewell, and C. Weik for GIS support. M. Cattet, N. Caulkett, B. Goski, J. Lee, M. Urquhart, and numerous Alberta Conservation Officers provided support during bear capture. Lastly, we thank R. Munro for her expertise in programming and management of radiocollars and GPS data, as well as her discussions on grizzly bear biology and conservation. Rick Bonar provided helpful comments and suggestions that improved the manuscript.

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