

Research Article

Seismic cutlines, changing landscape metrics and grizzly bear landscape use in Alberta

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Abstract

Besides providing habitat to the grizzly bear (*Ursus arctos*) and other wildlife, the Rocky Mountain foothills of Alberta, Canada hosts considerable mining, seismic oil and gas exploration and production, and forest harvesting activities. Worldwide, such human activities influence the configuration and composition of the landscape. We assessed seismic cutline effects on landscape structure and grizzly bear use during early summer of 1999 and 2000. We studied five female and two male bears, which were GPS-collared in the spring following den emergence. The area available to this population was stratified into 49 km² hexagon-shaped sub-landscapes. The scale of this stratification was determined by patterns of bear movement. Fourteen compositional and configurational landscape metrics were calculated within each landscape unit, and bear use points were pooled or ‘binned’ within each unit. Landscape use was related to landscape metrics using a Generalized Linear Model (GLM). We found that seismic cutline proportion did not explain landscape use by grizzly bears; however secondary effects of cutlines on landscape structure did. Declining use was mainly associated with increasing proportions of closed forest, and increasing variation of inter-patch distances, while use was mainly increasing with increasing mean patch size. An earlier investigation had demonstrated that adding seismic cutlines to grizzly bear habitat caused increases in the variation of inter-patch distances. Since the landscape structure of this grizzly bear population will continue to change as a function of increased levels of resource extraction activities in the near future, it is crucial to further study the detailed meaning of landscape structure at the large and small scale for effective conservation efforts.

Introduction

Wildlife and habitats are affected by human activity; this is true on a global scale and has been

among the key themes in Landscape Ecology (Forman 1997). The Rocky Mountain foothills of Alberta, Canada are among the vital locations in North America that provide habitat for grizzly

bears (*Ursus arctos*) and other wildlife. However, this area also hosts considerable mining, seismic oil and gas exploration and production, forest harvesting activities, and recreational activities, which inherently influence the configuration and composition of the natural landscape. For instance, in the process of conventional oil and gas exploration, a dense network of 5–10 m wide seismic cutlines is created. These cutlines dissect contiguous landscape components, or *patches*, thereby adding greatly to the fragmentation of this landscape (Linke 2003; Linke and Franklin 2003). Other human activities, such as forest harvesting, shape the landscape structure in direct ways, but also in indirect ways, for instance through the addition of roads (Reed et al. 1996; McGarigal et al. 2001). Managing the foothills grizzly bear population within this dynamic, multi-use landscape requires greater understanding of their habitat use within the landscape (Nielsen et al. 2002a) and the influences that landscape structure may have on such use. It is in this context that the Foothills Model Forest (FMF) Grizzly Bear Research Project was founded in 1999, with the objective to provide resource managers with the necessary knowledge and planning tools to ensure the long-term conservation of grizzly bears in the Yellowhead Ecosystem (Stenhouse and Munro 2000).

Relationships between spatial patterns and wildlife habitat processes have received much attention in the disciplines of environmental management, conservation biology, and landscape ecology over the last two decades (Wiens 1989; Levin 1992; Diaz 1996; Davidson 1998). Landscape metrics and indices have been developed to quantify spatial patterns into single variables (e.g., McGarigal and Marks 1995; Frohn 1998). These metrics can quantify the habitat from mere composition (i.e., proportion of habitat patches within a landscape unit, habitat richness and diversity) to actual configuration (arrangement, position and orientation of habitat patches within the landscape) (McGarigal and Marks 1995). Several studies have successfully related landscape metrics to habitat use and habitat selection of several wildlife species (e.g., Stuart-Smith et al. 1997; Chapin et al. 1998; Knutson et al. 1999; Potvin et al. 2001). Learning how habitat structure affects habitat use by wildlife can be very informative and is required for landscape conservation and

management. However, often it is unknown how anthropogenic development and disturbances affect large-scale habitat use by wildlife. What can be readily quantified though is how habitat structure is affected by human development, and appropriate relationships can then be formulated. Here we propose that knowing how human development affects landscape structure consequently will allow us to infer how wildlife will use habitat in these areas. This represents a new and innovative approach.

The outlined concept provides the mental framework of this study component of the FMF grizzly bear research project. In the foothills, oil and gas exploration is occurring at a remarkable rate (Schneider et al. 2003), which requires documentation of its consequences on grizzly bear landscape use. So far, only one small-scale study (12 km² large study area) investigated that the development of seismic cutlines did not displace grizzly bears in the Flathead River drainage in direct ways (McLellan and Shackleton 1989). For the first time, and in order to assess the existing findings further, we here undertake a large-scale study, investigating whether grizzly bear landscape use is affected by seismic cutlines and by the landscape structures they create in the East Slopes of the Rocky Mountains in Alberta. We offer a technique to address this growing resource management issue.

While previous grizzly bear habitat (GBH) studies have investigated habitat selection at scales varying from annual home ranges (Mace et al. 1996) to microsites (Hamer and Herrero 1987; Mace et al. 1996), several recent studies (Mace et al. 1999; Nielsen et al. 2002a) have focused on selection at a patch-level scale (Johnson 1980). These studies use a generalized linear model (GLM), which is the most commonly applied method for resource selection function (RSF) analysis (Manly et al. 1993; Boyce and McDonald 1999). RSFs have been developed for both individuals and populations (Mace et al. 1999; Nielsen et al. 2002a). This analysis can explain small-scale selection, preference and avoidance for patch or habitat types if the accuracy of utilization points is relatively high (White and Garrott 1990). However, we only find a few studies applying these habitat selection concepts to grizzly bear occurrence and to structural variables of the landscape. Two studies have focused on landscape composi-

tion, such as habitat proportion (McLellan and Hovey 2001) in the Flathead River drainage and habitat variety/richness in FMF grizzly bear RSF modeling (Nielsen and Boyce 2002). One study has reported its first findings on the investigation of configurational metrics, such as edge density, mean patch size (MPS), mean nearest neighbor and patch size covariance, in determining grizzly bear density classes of bear management units (BMUs), which are delineated watersheds in the rough size of a female annual homerange, in the FMF grizzly bear project (Poppellwell et al. 2003).

There appears to be a lack of a general consensus of the role of fragmentation and spatial patterns to grizzly bear ecology. Nielsen and Boyce (2002) demonstrated that grizzly bears selected for patches within a neighborhood of higher habitat variety. This is indicative of natural fragmentation since they would provide more potential local resources for various behavioral activities (e.g., feeding, bedding, etc.). However, anthropogenic fragmentation such as caused by roads has been demonstrated to trigger habitat avoidance of grizzly bears (McLellan and Shackleton 1988). While some of the detrimental effects of this fragmentation are the functioning of roads as barriers or even sinks (Gibeau 2000), the role of seismic cutline fragmentation is unknown. It could be proposed that individual seismic cutlines provide food or movement corridors for individual grizzly bears. On a large scale however, a network of seismic cutlines could have negative effects on population level landscape use of grizzly bears by dissecting contiguous habitat. The meaning of landscape structure to grizzly bear populations is far from solved.

In this study, we present a landscape ecology approach using a large-scale analysis to investigate what role seismic cutlines and landscape structure play in determining the landscape use of grizzly bears in the Alberta Rocky Mountain foothills. In our work, the bear population is considered to occupy a 'landscape mosaic' (Forman 1997), within which each sub-landscape has a different configuration and composition of landscape elements, or habitat patch types. The scale of the sub-landscapes is determined by the spatial autocorrelation of grizzly bear population use points, which are pooled, or 'binned' (Huettmann and Diamond 2000) into these sub-landscapes. This scale is assumed to be analogous to the scale of movement of the sampled bear population, mini-

mizing the autocorrelation of binned use points between sub-landscapes.

Our analysis focused on the early summer (June 1–July 31) time window, to reduce seasonally influenced foraging behavior effects (Nielsen et al. 2002b). In Western–Central Alberta, grizzly bears tend to hibernate until April or May, with male bears emerging before female bears. Then during early summer, bears are known to feed on a variety of foods, such as horsetail (*Equisetum arvense*), cow parsnip roots (*Heracleum maximum*), graminoids (grasses, sedges and rushes), insects, and on elk calves or carrion (Herero 1985; Hamer and Herrero 1987; Nagy et al. 1989; Munroe and Stenhouse 2003). We selected this time period since the foraging behavior is considered more general and the food supply is more evenly distributed. This period stands in contrast to late summer and early fall, when the foraging behavior is mainly driven by berries, such as buffalo berries (*Shepherdia canadensis*) and blueberries (*Vaccinium* spp.) (Hamer and Herrero 1987; Nagy et al. 1989) and thus presenting a different underlying distribution 'mechanism', which is not part of the objective of this investigation. However, a follow-up study should investigate this season further in order to complement the understanding for the entire annual cycle of the bear population.

Study area and methods

Study area

This study was carried out in the eastern portion, the foothills zone, of the FMF Grizzly Bear Project (Stenhouse and Munro 2000), located within the Yellowhead Ecosystem, southwest of Hinton, Alberta, Canada (Figure 1). The western portion of the FMF Grizzly Bear Project falls within Jasper National Park, where no human use related to resource extraction exists. Bio-geoclimatic conditions, grizzly bear food production and availability differ between the park and the foothills zone preventing comparisons between the multi-use foothills zone and the protected park zone. Therefore, this study was restricted to the multi-use foothills zone, where anthropogenic disturbance exists throughout, however to varying degrees. The 3040 km² foothills zone includes a range in topographic elevation from about 1010 to

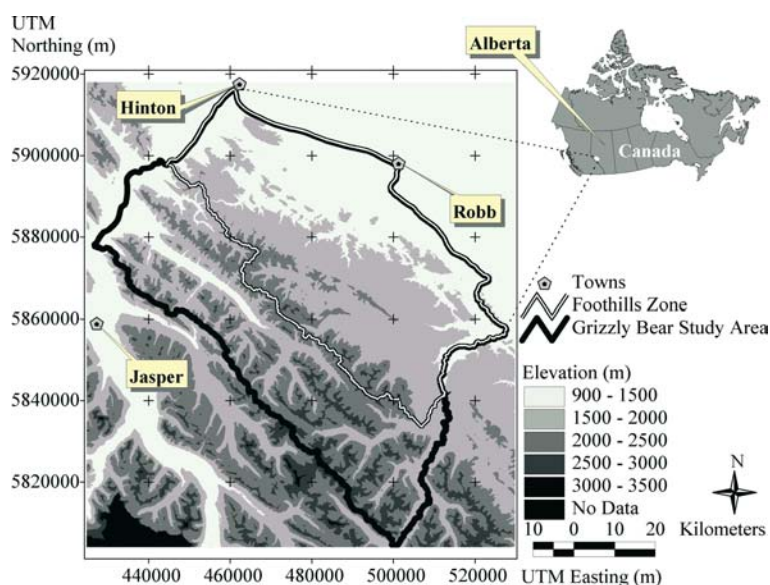


Figure 1. The foothills zone study area within the FMF Grizzly Bear Research Project area, Alberta, Canada, in context of topographic gradients, and major towns (UTM Zone 11).

2880 m, with about 25% of the area contained in the alpine region and the remaining 75% in the upper foothills of the eastern slopes of the Rocky Mountains.

Research design

We investigated the relationship between landscape structure and different levels of landscape use from global positioning system (GPS)-collared grizzly bears during early summer for each of 2 years (1999 and 2000). We used multi-variate regression analysis to model these relationships. In addition to the investigation of the total sample population, we also examined the relationships separately for males and females, in order to estimate their relative contributions to the sample population under study. The extent of this investigation was determined by the cumulative, non-overlapping 100% minimum convex polygon (MCP) (White and Garrott 1990) of early summer GPS points of individual bears. This reflects the area available to the sample population. The available area was subsequently divided into sub-landscapes at a resolution or grain, which is determined by the spatial autocorrelation of GPS points of all bears.

Grizzly bear data

GPS location data

In order to collect detailed movement and habitat use data on grizzly bears within the study area, it was necessary to capture, immobilize, and radiocollar a representative sample of the grizzly bear population. Capturing effort was equally distributed across all BMUs within the FMF Grizzly Bear Project to ensure adequate representation of the overall population. All capture efforts taking place in this program followed procedures outlined by the Canadian Council on Animal Care for the safe handling of bears (in review). In 1999 and 2000 respectively, 19 and 20 adult (≥ 5 years old) and subadult (3–5 years old) grizzly bears were captured and collared. This was done throughout the FMF Grizzly Bear Project with either a 12-Channel Televilt (Lindesburg, Sweden) GPS-Simplex radiocollar, or an ATS (Advanced Telemetry Systems, Isanti, Minnesota) GPS radiocollar. The radiocollars were programmed to record locations every 4 h, with a spatial accuracy of about 10–20 m.

Using a Geographic Information System (GIS) (Arcview Version 3.2), 100% MCP home ranges for each bear were computed from GPS locations (Hooge and Eichenlaub 1997). For this study, we

selected collared bears having their annual home range area contained within the foothills zone, since inferences were to be drawn from the full area available to the sampled population. Two males and five females collared bears qualified for this restriction over the 2-year period, with three females (bears G004, G016, and G020) being represented in both years (Table 1). We had classified every sample bear according to its exposure to human use related to resource extraction into three categories (low, medium and high) based on the amount of roads, harvesting, seismic and mining activities within each home range, but not on the actual amount of recreational use (Nielsen and Boyce 2002). The sample population of bears had roughly equal numbers in every category (Table 1). The number of retrieved GPS locations ranged between 131 and 300 per individual during the early summer season (Table 1).

Except for a known association event between bears G016 and G008 at the end of June 1999 (Stenhouse et al. 2004), for which time period GPS locations were removed from the data set, we did not account for any mating behavior.

Scale of analysis

To stratify the foothills zone study area into sub-landscape units of equal size and shape, we used the scale at which the sampled grizzly bear population apparently operated over the 2-year period of the GPS sampling. We determined the distance at which strong autocorrelation existed between all early summer sample bear locations using Ripley's *K* Statistic. In contrast to first-order point pattern statistics, such as nearest neighbor analysis, which

quantify the mere, large-scale, mean spatial trend of point data regardless of small-scale pattern intensity and scale, Ripley's *K* is a second-order point pattern statistic, designed to detect spatial clustering or autocorrelation over distance classes (Ripley 1976; Venables and Ripley 1997; Fortin 1999). We used the Crimestat Software (Levine 1999) implementation for the Ripley's *K* analysis. The distance after which bear locations become less clustered was used to guide the scale of movement for each year's population. The clustering distances for the early summer season in the years 1999 and 2000 were 8.7 and 6.9 km, respectively; however, in order to fit both populations to the same scale, the larger 8.7 km distance was selected since it appeared to encompass both movement patterns from both years. We then delineated hexagons with an 8.7 km diameter (49 km²); while a circle represents the ideal landscape unit with the radius being equal in all directions, a series of circles cannot practically be packed together without wasted space (Laurin and Thompson 1992).

Grizzly bear landscape use

To characterize bear landscape use, we 'binned' each year's bear population locations within a landscape unit (49 km² hexagon) (Figure 2). Binning is a spatial method used to group data or samples by regular spatial units (bins) (Huettmann and Diamond 2000). We adjusted bin counts for the actual area available to the population, as indicated by the early summer population MCP homerange boundary. This method yielded bear use densities per sub-landscape. Sub-landscapes

Table 1. Sex, age, number of GPS locations, exposure to human use related to resource extraction, and 100% MCP home range sizes for each GPS collared grizzly bear located within the foothills zone of the FMF Grizzly Bear Research Project area during early summer (June 1–July 31) of 1999 and 2000.

Bear number (ID)	Sex	Age in 1999	Exposure to human use	Number of GPS locations		Early summer homerange	
				1999 (<i>n</i>)	2000 (<i>n</i>)	1999 (km ²)	2000 (km ²)
G004	Female	5	Low	300	183	154	228
G005	Male	11	Medium	282	–	1116	–
G008	Male	14	Medium	201	–	979	–
G011	Female	6	Medium	–	140	–	154
G016	Female	5	Low	230	131	153	51
G020	Female	4	High	190	142	276	397
G023	Female	11	High	–	199	–	362
All bears (cumulative area)	–	–	–	1203	795	1457	1053

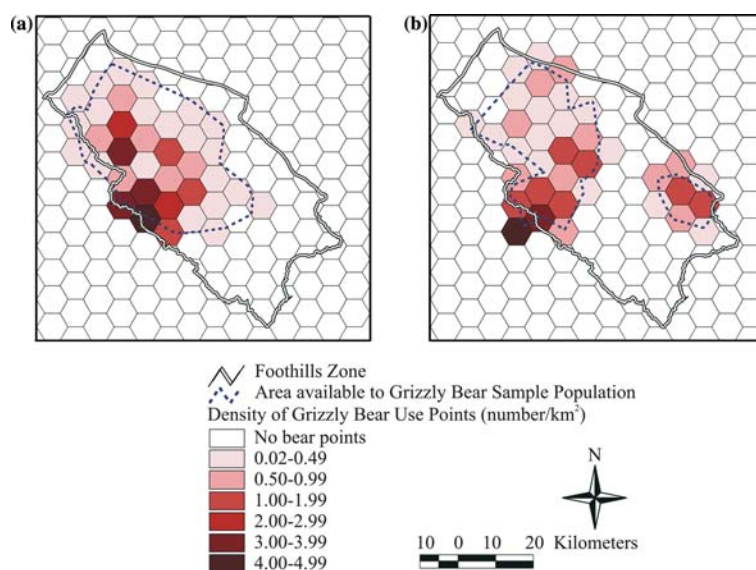


Figure 2. Stratification of the study area into movement scale (8.7 km diameter), hexagon-shaped sub-landscapes and corresponding density of collared grizzly bear use points in relation to available area during early summer of (a) 1999 and of (b) 2000.

falling within the available area but lacking any use points were not included in this investigation, since the objective was to explain levels of population use rather than presence or absence. A total of 72 sub-landscapes over the 2 years was the result of this procedure. Due to the autocorrelation-based scale of analysis, homogeneously sized sub-landscapes existed, which were independent of neighboring sub-landscapes.

Remote sensing and GIS data

Landscape cover

As the source data for landscape structure quantification, we used 30 m spatial resolution land cover maps for the years 1999 and 2000 (for a review see Gottschalk et al. 2005). These maps were created based on an integrated decision tree approach (IDTA) to classifying Landsat satellite imagery (Franklin et al. 2001). The 23 IDTA landcover types (Table 2) had an overall accuracy of 83% (Franklin et al. 2001). Roads were part of the IDTA map, which combined all undivided paved roads, to one-lane gravel, and unimproved roads. Seismic explorative and exploitative cutlines were merged into the IDTA landcover map. These features were obtained by digitizing 5 m resolution Indian Remote Sensing (IRS) Satellite Imagery

from 1998; the accuracy of this data set was 88% (Linke 2002, 2003). The detailed IDTA maps were subsequently reclassified into a more general GBH map with 16 landcover types (Table 2) to reduce the number of variables (Popplewell 2001).

Streams and elevation

Nielsen et al. (2002a) have demonstrated relationships between GBH selection and distance to stream suggesting the incorporation of stream density in this analysis. Since only major streams were part of the IDTA landscape cover map, the total length of perennial and intermittent streams per landscape unit was compiled from a GIS. Elevation was obtained from a 100 m Digital Elevation Model (DEM). We computed the standard deviation of elevation for each sub-landscape as an index of vertical ruggedness (Evans 1972) using Spatial Analyst in Arcview GIS.

Landscape structure assessment

Using Fragstats 3.1 software build 3 (McGarigal et al. 2002), we calculated several landscape metrics, quantifying all possible aspects of landscape structure such as area/edge density, shape, nearest neighbor, contrast, contagion/interspersion, and diversity metrics, from the GBH map for

Table 2. Landcover types from the IDTA map, the reclassified GBH map, and the final reclassification of landcover types for landscape composition calculations.

IDTA landcover types	GBH landcover types	Final reclassification of landcover types for landscape composition calculation
Closed conifer	Closed conifer	Closed forest ^a
Closed deciduous	Closed deciduous	
Mixed forest	Mixed forest	Open forest ^a
Open conifer	Open conifer	
Open deciduous	Open deciduous	Alpine
Alpine	Alpine	
Herbaceous < 1800 m	Herbaceous < 1800 m	Herbaceous ^a
Shrub < 1800 m	Shrub < 1800 m	Shrub and Wetlands ^a
Wet open	Wetland	
Wet-treed		
Rock	Non-forested features	Non-forested features
Snow		
Shadow		
Water		
Urban		
Pipeline	Wellsites and pipeline	
Wellsite		
Roads/rail	Roads/rail	Roads/rail ^a
Recent cut	Recent cut	Recent cut ^a
Cut 3–12 years	Older cut	Older cut ^a
Cut > 12 years		
Cut unknown age		
Recent burn	Recent burn	Recent burn ^a
Seismic lines	Seismic lines	Seismic lines ^a

^aUncorrelated cover types used in the analysis.

each of the 72 sub-landscapes. The metrics were computed at the landscape level, measuring the aggregate properties of the entire habitat patch mosaic (McGarigal et al. 2002) for each sub-landscape. Individual grid cells of the same landcover type were aggregated to form individual patches, using an 8-cell (Queen's case) patch neighbor rule (McGarigal et al. 2002). Landscape background and border were not counted as edges since these do not represent true but artificial edges. To efficiently calculate composition of each landscape unit (i.e., proportion of landcover type), we simplified the 16-class GBH map into 11 cover type classes (Table 2), some of which were also used in other GBH studies (Mace et al. 1996; Waller and Mace 1997; Nielsen et al. 2002a).

Since multivariable regression analysis is sensitive to collinearity among predictor variables (Harrell 2001), we removed correlated landscape metrics ($r > 0.6$) in a hierarchical approach. Only those metrics with the least number of collinear landscape metrics were retained. Four configurational landscape metrics were uncorrelated, which

included mean patch size (MPS), mean shape index (MSI), coefficient of variation in mean nearest neighbor (MNN_CV), and Simpson's Evenness Index (SIEI). Two of the 11 landcover type proportions, 'alpine' and 'non-forested features', were removed from the data set since they were correlated with several other types. 'Alpine' was correlated with 'closed forest' ($r = -0.65$), with 'open forest' ($r = 0.66$), and with 'non-forested features' ($r = 0.63$). 'Non-forested features' was also correlated with 'closed forest' ($r = -0.66$). The ruggedness index was also removed from this investigation, since it was correlated with proportion of seismic lines ($r = -0.71$), and seismic lines constituted one of the major landscape variables of interest. The final set of landcover type proportions entering the statistical analysis were those of closed forest (Pclforest), open forest (Popforest), herbaceous cover (Pherb), shrubs and wetlands (Pshrubs), roads (Proads), recent clearcuts (Precentcut), older cuts (Poldcuts), fire-originated stands (Pburn), seismic lines (Pseismic), and streams (Pstreams).

Statistical analysis

We used Poisson family GLM with log-linear link (Venables and Ripley 2002) to relate the 14 independent ($r < 0.6$) landscape metrics (four configurational and 10 compositional metrics) for each landscape unit with the grizzly bear landscape used by all sampled bears (population-level), by all sampled females, and by all sampled males. It was visually confirmed that the bear landscape use data was poisson distributed, and GLMs extend the assumptions of normality associated with classical linear regression modeling to accommodate such non-normal response variables (McCullagh and Nelder 1989; Quinn and Keough 2002). We limited our investigation to linear relationships to reduce model complexity.

The underlying strategy of our investigation was to find the best-fitting explanatory models with the smallest number of predictor variables, following the principle of parsimony (Box and Jenkins 1970; Burnham and Anderson 2002; Quinn and Keough 2002). We modified the S-PLUS code approach from Huettmann and Linke (2003) to formulate candidate models based on widely applied backward stepwise model elimination starting with the global model of landscape variables in the following order: MPS, MSI, MNN_CV, SIEI, Pelforest, Popforest, Pherb, Pshrubs, Proads, Precentcut, Poldcut, Pburn, Pseismic, Pstreams. To ease the interpretation and comparability of regression coefficients, predictors were standardized to z -scores by calculating the deviations from the mean in standard deviation units previous to regression analysis (Menard 2001; Quinn and Keough 2002).

In order to identify the set of parsimonious models explaining grizzly bear landscape use, the Akaike's Information Criterion for small sample sizes (AIC_c), the AIC differences (Δ_i) and Akaike weights (w_i) (Burnham and Anderson 2002) were used. All candidate models ranked higher than the null model were presented. Using Δ_i between 0 and 2 as a guide, best-fitting models were selected to explain grizzly bear landscape use (Burnham and Anderson 2002). Coefficients, standard errors and percent of the explained deviance of all best-fitting models were calculated. All statistical data handling was done using S-PLUS 2000 (Mathsoft 1999) on an IBM PC computer.

Results

Population-level landscape use

Landscape structure variables had wide ranges among the sub-landscapes throughout all three levels of analysis (Figure 3). This indicates that the foothills grizzly bears occupy a heterogeneous landscape. When we related the sampled population of seven bears over 2 years to all 14 landscape structure variables within 72 consistently sized sub-landscapes, six models were identified as better than the null model based on their contribution to reducing the model AIC_c (Table 3). Among these, four explanatory, GLMs were selected as best suited (Table 3). While MPS was ranked as the first best model, the three other highest-ranked, competing models identified MNN_CV, and Pforest as additional, important explanatory landscape variables (Table 3). Overall, these competing models explained between 13.8 and 36.7% of the deviance (Table 4). The coefficients of the four models were consistent and overall suggest that landscape use of collared foothills grizzly bears increases with increasing MPS, and that it decreases with increasing variation in mean nearest neighbor distances among similar patches (MNN_CV), and with increasing proportions of closed forest (Pelforest). The proportion of seismic lines (Pseismic) within the landscape was not selected in any explanatory model for the population-level landscape use.

Sex-specific population-level landscape use

The relationship between sex-specific sample landscape use and landscape structure was also investigated in order to isolate their contributions to the overall population-level model. Eighteen candidate models were identified above the null model of female landscape use based on the model AIC_c (Table 5). Among these candidate models, five models were identified as best explaining female population-level landscape use (Table 5). Similarly to the population-level analysis, MPS, MNN_CV, and Pforest were identified as important predictors of female landscape use across the five competing models (Table 5). The models also identified the landscape variables MSI, SIEI, and Popforest as important predictors

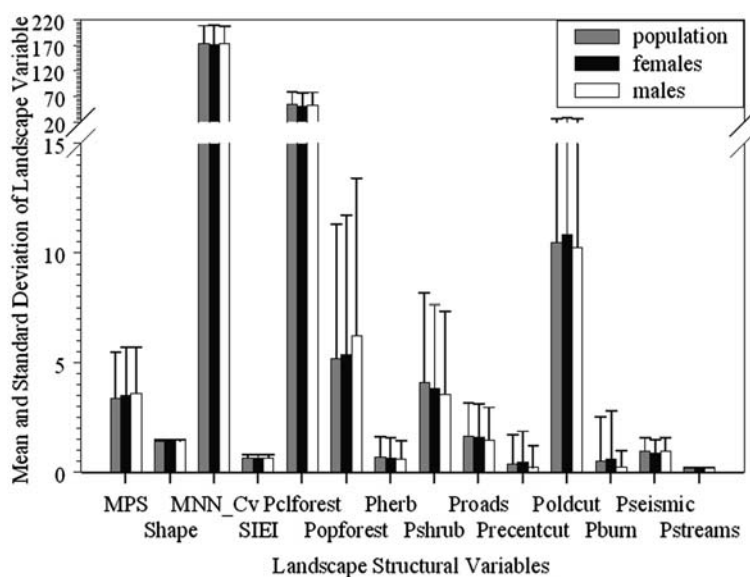


Figure 3. Mean and standard deviation of landscape structure variables, such as MPS, MSI, MNN_CV1, SIEI, Pclforest, Popforest, Pherb, Pshrubs, Proads, Precentcut, Poldcuts, Pburn, Pseismic and Pstreams over all sub-landscapes within the sample population-level ($n = 72$ sub-landscapes), the female sample population-level ($n = 61$ sub-landscapes), and the male sample population-level analysis ($n = 35$ sub-landscapes).

Table 3. Six candidate models (GLM, Poisson family) for grizzly bear landscape use (total population) in the foothills zone of the Rocky Mountains of Alberta (early summer of 1999 and 2000).

Rank	Candidate models	AIC _c	Δ_i	w_i
1	MPS^a	192.85	0.00	0.36
2	MPS, Pclforest^b	193.64	0.79	0.24
3	Pclforest	194.32	1.48	0.17
4	MPS, MNN_Cv^c Pclforest	194.71	1.87	0.14
5	MPS, MSI ^d , MNN_Cv, SIEI ^e , Pclforest	197.03	4.19	0.04
6	MNN_Cv, Pclforest	197.05	4.21	0.04

The models performed better than the null model (null model AIC for small sample sizes AIC_c = 197.23) and are shown in decreasing order of importance based on the AIC_c, with the AIC difference (Δ_i) and the Akaike weights (w_i). The best-fitting models are displayed in bold.

^aMean patch size.

^bProportions of closed forest.

^cCoefficient of variation of mean nearest neighbor distances.

^dMean shape index.

^eSimpson's evenness index.

(Table 5). These competing models explained between 27.9 and 30.1% of the deviance and the model coefficients were consistent across all five models (MPS is slightly negative in two female models, but due to large standard errors, it reaches well into the positive values and is therefore in agreement with the other models) except for MPS (Table 4). Overall, the competing models indicated increasing use with increasing MPS, and decreasing

use with increasing MSI, MNN_CV, SIEI, Pclforest, and Popforest (Table 4).

When relating the male population-level grizzly bear landscape use to the landscape structure variables, only one model (AIC_c = 70.8) was identified as better than the null model (AIC_c = 71.75). This model selected MPS as the only variable important for male landscape use with its coefficients in support of the population level

Table 4. Coefficients (β), standard errors (SE), residual degrees of freedom (DF), and percent explained deviance (ED) of the best AIC selected models for grizzly bear landscape use (total sample population, female and male sample) during early summer of 1999 and 2000 in the foothills of the Rocky Mountains, Alberta.

Bear sample	Model details	1st ranking		2nd ranking		3rd ranking		4th ranking		5th ranking	
		model	model	model	model	Model	model	model	model		
	Variables:	β	SE	β	SE	β	SE	β	SE	β	SE
Population	MPS ^a	0.32	0.10	0.03	0.13			0.16	0.14		
	MNN_Cv ^b							-0.26	0.14		
	Pelforest ^c			-0.53	0.17	-0.56	0.13	-0.44	0.17		
	Intercept	-0.22	1.33	-0.32	0.15	-0.32	0.15	-0.34	0.15		
	DF	70		69		70		68			
	ED (%)	13.8		30.7		30.6		36.7			
Females	MPS	0.06	0.14			-0.03	0.23	-0.03	0.23	0.12	0.15
	MSI ^d					-0.12	0.15	-0.13	0.16		
	MNN_Cv					-0.09	0.15	-0.09	0.16	-0.13	0.13
	SIEI ^e					-0.19	0.23	-0.20	0.24		
	Pelforest	-0.41	0.17	-0.46	0.13	-0.49	0.23	-0.49	0.23	-0.37	0.18
	Popforest ^f							0.01	0.16		
	Intercept	-0.12	0.14	-0.12	0.14	-0.14	0.14	-0.14	0.14	-0.13	0.14
DF	58		59		55		54		57		
	ED (%)	27.9		27.5		33.9		34.1		30.1	
Males	MPS	0.16	0.25								
	Intercept	-1.00	0.28								
	DF	33									
	ED (%)	2.6									

^aMean patch size.

^bCoefficient of variation of mean nearest neighbor distances.

^cProportions of closed forest.

^dMean shape index.

^eSimpson's evenness index.

^fProportion of open forest.

analysis (Table 5). The coefficient suggests that male landscape use increases with increasing MPS (Table 5). However, the low explanatory power of this model of 2.6% and in absence of other competing models, suggests that male landscape use remains largely unexplained (Table 5).

Discussion

This analysis offers a case study to investigate and address a growing resource management issue for wildlife habitat and its modifications in North America. Despite the lack of quantitative support for habitat displacement, McLellan and Shackleton (1989) suggested potential detrimental effects by seismic cutlines when considering habitat alteration, garbage management and improved landscape access. Our study also showed no direct relationship between the proportion of seismic cutlines and population-level landscape use.

However, a critical link between seismic cutlines and grizzly bear landscape use has been established in indirect ways: by means of landscape metrics, which quantify the issue of habitat alteration. In the absence of accounting for foraging, bedding and grizzly bear behaviors important during early summer, such as mating in our study (Stenhouse et al. 2005), we were able to explain a considerable portion (up to about 37% of the deviance) of the population-level landscape use alone by three landscape metrics; overall, use increased with increasing MPS, and it decreased with increasing proportions of closed forest, and with increasing variation in mean nearest neighbor distances between patches of the same habitat type over the available area to the studied population.

Previous investigations of the effects of adding seismic cutlines to GBH revealed significant, direct relationships between cutline densities and several configurational landscape metrics (Linke 2003;

Table 5. Eighteen candidate models (GLM, Poisson family) for grizzly bear landscape use (females) in the foothills zone of the Rocky Mountains of Alberta (early summer of 1999 and 2000).

Rank	Candidate Models	AIC _c	Δ_i	w_i
1	MPS^a Pclforest^b	144.00	0.00	0.24
2	Pclforest	145.09	1.09	0.15
3	MPS, MSI^c MNN_CV^d SIEI^e Pclforest	145.13	1.13	0.14
4	MPS, MSI, MNN_CV, SIEI, Pclforest, Popforest^f	145.65	1.65	0.11
5	MPS, MNN_CV, Pclforest	145.98	1.98	0.09
6	MNN_CV, Pclforest	146.74	2.74	0.06
7	MPS, MSI, MNN_CV, SIEI, Pclforest, Popforest, Pherb ^g	147.07	3.07	0.05
8	MPS, MSI, MNN_CV, SIEI, Pclforest, Popforest, Pherb, Pshrubs ^h	147.08	3.08	0.05
9	MPS	148.03	4.03	0.03
10	MPS, MSI, MNN_CV, SIEI, Pclforest, Popforest, Pherb, Pshrubs, Proads ⁱ	148.37	4.37	0.03
11	MPS, MSI, MNN_CV, SIEI, Pclforest, Popforest, Pherb, Pshrubs, Proads, Precentcut ^j	150.21	6.21	0.01
12	MPS, MNN_CV	151.61	7.61	0.01
13	MPS, MSI, MNN_CV, SIEI, Pclforest, Popforest, Pherb, Pshrubs, Proads, Precentcut, Poldcut ^k	151.95	7.95	0.00
14	MPS, MSI	152.20	8.20	0.00
15	MPS, MSI, MNN_CV	152.42	8.42	0.00
16	MPS, MSI, MNN_CV, SIEI	153.46	9.46	0.00
17	MPS, MSI, MNN_CV, SIEI, Pclforest, Popforest, Pherb, Pshrubs, Proads, Precentcut, Poldcut, Pburn ^l	154.40	10.45	0.00
18	MNN_CV	154.85	10.85	0.00

These models performed better than the null model (null model AIC for small sample sizes AIC_c = 154.54) and are shown in decreasing order of importance based on the AIC_c, with the AIC difference (Δ_i) and the Akaike weights (w_i). The best-fitting models are displayed in bold.

^aMean patch size.

^bProportions of closed forest.

^cCoefficient of variation of mean nearest neighbor distances.

^dMean shape index.

^eSimpson's evenness index.

^fProportion of open forest.

^gProportion of herbaceous cover.

^hProportion of shrubs and wetlands.

ⁱProportion of roads.

^jProportion of recent clearcuts.

^kProportion of older cuts.

^lProportion of fire-originated stands.

Linke and Franklin 2003). Additional kilometers of seismic cutlines caused percent decreases in MPS and percent increases in variation of mean nearest neighbor distances (MNN_CV) (Linke 2003). Similar direct impacts on landscape configuration have also been recorded in the study of roads over time (McGarigal et al. 2001).

Our study suggests that the investigated grizzly bear population does not respond to seismic cutline densities in early summer, but to the habitat structure they create. Bears appear to use areas more when landscape patches tend to be larger, and MPS is generally reduced with additional seismic cutlines (Linke 2003; Linke and Franklin 2003). Also, bears appear to use areas more when landscape patches are consistently spaced, and the spacing between landscape patches becomes more variable with additional seismic cutlines (Linke

2003). The variation in mean nearest neighbor distances among similar patches (MNN_CV) is an important, explanatory metric in this investigation, which can be affected by landscape extent over which it is assessed. This sensitivity to scale, however, does not affect the inferences drawn in this analysis, since the extent of the individual sub-landscapes was consistent over the entire area.

Whereas Nielsen and Boyce (2002) demonstrated that grizzly bears tended to select for areas with higher habitat variety, which suggests patchy landscapes, we can contribute that the studied grizzly bear use appears to decrease, if the habitat patches occur at more variable distances to each other. Hamer and Herrero (1983) already also suggested the importance of habitat patch configuration in context of grizzly bear movement by summarizing that grizzly bears appeared to move

frequently between similar habitat patches. These authors state that grizzly bears “abandon seemingly abundant food source for opportunities farther afield (and) often the bear’s new location has the same food items in the same habitat type”. While grizzly bears appear to generally forage at a small-scale, there are implications of the large-scale structuring of the landscape. A more consistent spacing between habitat patches could indicate lower energetic cost on the search for food, resting or bedding, which would make such a landscape condition more suitable for grizzly bear persistence. Our results are also consistent with other research in Montana, British Columbia, and Alberta which has shown a more frequent, stronger association between grizzly bears in open vs. closed forested habitats (Servheen 1983; Herrero 1985; Hamer and Herrero 1987; Waller and Mace 1997; Nielsen et al. 2002a). General road avoidance was found in several other areas of the grizzly bear range, such as Wyoming (Mattson et al. 1987), southern British Columbia (McLellan and Shackleton 1988), and Montana (Mace et al. 1996, 1999). While roads were not identified as an important predictor in the parsimonious models for grizzly bear landscape use, it was found that proportion of roads was negatively correlated with MPS ($r = 0.55$). Since grizzly bear landscape increased with increasing MPS, a negative relationship between landscape use and proportion of roads could also be inferred in this study. The selection for patches of average larger sizes is consistent with the general description of the grizzly bear’s need to roam large spaces.

Based on our sex-specific bear population-level analysis, we found that the female sample mainly drove the declining landscape use associated with increasing proportion of closed forest and increasing variation of mean nearest neighbor distances, while male landscape use remained largely unexplained. Analyzing females separately from the total population revealed that female landscape use was also affected by MSI and SIEL. However, the coefficients of these landscape variables fluctuated with standard errors being too large to infer meaningful clear relationships. At the investigated scale of analysis, this could indicate that males act as generalists at the population-level, not responding to spatial patterns, but rather to the general need to roam large spaces. The selected scale for sub-landscapes was also deemed

appropriate for investigating males as a separate population, since the Ripley’s K analysis of all male GPS locations during early summer indicated a scale of movement of 8.4 km.

The inferences made above need to be considered with caution and in the context of the underlying population composition and sampling details. The sample population was balanced in its relative exposure to human use related to resource extraction. However, it was not balanced in respect to seasonal home range sizes, numerical contribution of GPS locations, and sex (Table 1). A female bias in the analyzed population existed and within the female group, some individuals were represented by more GPS locations than others. Since the bear capturing efforts had been distributed approximately equal across the study area, ensuring adequate representation of the local population, the inferences drawn from this sample are representative at the population level despite the unbalanced sex and home range characteristics. The positioning of the sub-landscapes over the foothills zone had been performed in a way to maximize the number of sub-landscapes over the area available to the bear sample population. Due to the relatively large sample of sub-landscapes and the large spread in landscape structure conditions over all sub-landscapes, we do not expect that the landscape structure relationships are sensitive to the positioning of this stratification, however, future studies should incorporate a full randomization procedure of this stratification.

This analysis was also subject to potential influences of GPS-collar bias, which dealt less with the spatial inaccuracy due to the 30 m habitat mapping resolution, but with missing data in the form of failed location attempts (Frair et al. 2004). Collar brand, steep slopes, and dense forest canopies can all contribute to lower probabilities of acquiring GPS locations as demonstrated by a study within the FMF Grizzly Bear Project boundary (Frair et al. 2004). Simulating a GPS bias related 10% location data loss revealed Type II errors, but no Type I errors or changes of signs in RSF coefficients. This finding by Frair et al. (2004) suggests that despite missing locations in our GPS data set, the final model variables explaining grizzly bear landscape use are not an artifact of the GPS collar bias. Also, the probability of Type II error occurrence in our analysis is unlikely, since the unselected model variables were

not associated with high canopy densities. Due to the inverse correlation between ruggedness, an indication of the amount of slopes per sub-landscape, and the model variable 'pseismic' ($r = -0.72$), the risk of the Type II error caused by steep slopes is improbable. The majority of collars were of Televilt brand, which have a lower probability of acquiring GPS locations than the ATS collars (Frair et al. 2004), but the population-level approach taken in this analysis is likely insensitive to this bias.

GIS data inaccuracies need to be considered as potential sources of introducing noise to the analyzed relationships. While the grizzly bear habitat maps had been updated annually, the seismic cutline data set used in this analysis had been derived from imagery of the year 1998. When field-tested in summer 2001, the errors of omission and commission of this data set was assessed to be fairly low, being 12 and 4%, respectively (Linke 2003). Given these accuracy assessment results, more seismic cutline densities were underestimated than overestimated. This could have contributed to the lack of response of landscape use to seismic cutlines.

Our analysis approach appears to be most sensitive to strongly differing, early summer home range sizes. An individual with many GPS location points and a small home range (such as G016) becomes a strong driver for characterizing population-level landscape use. These locations will be pooled across a minimal number of sub-landscapes (bins) and cause higher use point densities than individuals whose locations are dispersed over a much larger range. This effect becomes apparent since the early summer home range of G016 falls partially within alpine habitat along the western border of the foothills zone. The proportion of alpine habitat was negatively correlated with the proportion of closed forest. Considering this relationship, we suggest that the strong avoidance of closed forest exhibited by the sampled population is influenced by G016's contribution to high-density sub-landscapes. In using this landscape ecology approach to relate spatial patterns to bear landscape use, it is important to define the sample population composition is crucial to obtaining viable results. Individuals need to be grouped in a representative fashion by sex, reproductive status, and especially GPS locations and home range size. Strong variation in habitat use among individuals is well known among large

mammals, and has previously been noted for this population (Nielsen et al. 2002a). We are accumulating more data sets on grizzly bears within the extended FMF Grizzly Bear Project study area in the years 2001–2003, which will provide an opportunity to test this method and design in more detail.

In this study, it has been demonstrated that landscape configuration, and not only habitat composition or type, matter to grizzly bear landscape use. Despite the lack of the full understanding of the impacts of landscape structure on grizzly bear populations at this stage, we have contributed a first and important step towards achieving this goal. We have established that seismic cutlines, a landscape feature associated with oil and gas exploration, modify the landscape in a way that appears to be less favorable for grizzly bear use. Cutlines change the configuration of the landscape; they increase the variation of inter-patch distances, while bear use is higher in areas with lower variation of this metric. The landscape structure of this grizzly bear population will continue to change as a function of increased levels of resource extraction activities over the near future. Therefore, it is crucial to further study the meaning of landscape structure at the large and small scale, so that conservation efforts can become more specific in this aspect.

Some particular recommendations are focused on individual-level grizzly bear landscape use applying similar approaches as demonstrated here. The individual's home range can define the available area to be stratified into sub-landscapes depending on the individual's movement pattern, and locations are binned inside those. Also, point-based, patch-level habitat selection of individual bears focusing on landscape metrics in their respective ecological neighborhood would reveal further preferences and avoidances for certain landscape configurations. Other landscape use variables, such as movement rates or residence indices (Turchin 1998), could also be investigated to reveal more information about the nature of grizzly bear use. We believe that the role of food distribution and its possible confounding effects with the landscape structure on grizzly bear landscape use during the entire annual cycle represents an investigation of major future importance. More integrative models incorporating landscape struc-

ture together with food availability, bedding and resting site availability, and mating behavior constitute the challenges of future grizzly bear modeling work.

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