MODELING GRIZZLY BEAR HABITATS IN THE YELLOWHEAD ECOSYSTEM OF ALBERTA: TAKING AUTOCORRELATION SERIOUSLY

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Abstract: We used resource selection functions (RSF) to estimate relative probability of grizzly bear (*Ursus arctos*) use for habitats, landscape features, and areas of varying human access density across a 5,342-km^2 study area in west-central Alberta, Canada. Models were developed based on 1999 data at both the population and individual levels for the spring and summer–autumn seasons. Individual-based RSF models revealed strong differences in selection among animals. Models developed for the summer–autumn season fit better than models of the spring season. High greenness values, derived from Landsat imagery, corresponded well with grizzly bear habitat use. Significance of parameters was frequently overestimated when using logistic regression models that were unadjusted for autocorrelation or pseudoreplication, both in individual-based models and in population-based models. Although not affecting predictability of bears at the individual-level, such biases may lead to inappropriate conclusions without adjustment. Population-based models further showed bias without correction for pseudo-replication within individuals (unit of replication). Consideration of variance inflation factors and nesting of telemetry points on the individual enhances the reliability of habitat modeling. We found problems predicting grizzly bear habitat use when local habitat index models were used. The RSF models presented here improve such models while also generating information on the contribution of particular environmental variables.

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Key words: Alberta, autocorrelation, greenness, grizzly bears, habitat modeling, habitat selection, logistic regression, pseudo-replication, resource selection functions, *Ursus arctos*, variance inflation factors

Faced with increasingly complex social–environmental landscapes, managers and conservationists are being asked for innovative strategies to manage and conserve rare, threatened, and endangered species. Such strategies require understanding of local essential resources (Leopold 1936). Resource selection functions (RSF) have been promoted as one statistically based technique (Manly et al. 1993) that provides this link. Although RSF models do not provide precise information regarding differential fitness among individuals (Garshelis 2000), the advantages of RSF models over some other techniques include their objectivity (vs. Delphi models), explanatory ability, and probabilistic nature. Maps resulting from such models are useful for resource management and conservation planning.

RSF models for grizzly bears have been developed for the Rocky Mountain Region of the United States (Mace et al. 1996, 1999; Boyce and Waller 2000). However, no such models exist for the Northeast Slopes Region of the Canadian Rockies in west-central Alberta. Spatially explicit probability maps and inferences regarding responses to human activity in these areas are especially relevant because local bear populations face substantial pressures from resource development (e.g., oil, gas, coal, timber; Nagy and Haroldson 1990, McLellan and Banci 1999, McLellan et al. 1999). One criticism of using a statistically based approach to predict habitat selection and response to disturbance has been the use of inappropriate designs (population vs. individual) and lack of attention to autocorrelation and pseudoreplication (Lennon 1999, Otis and White 1999). When true, these criticisms lead to questionable interpretations of model parameter significance and inference (Lennon 2000).

In this paper, we describe robust RSF models for an area known as the Yellowhead Ecosystem. We focus on patch-level selection (third-order processes; Johnson 1980) for both individuals and the population during 2 seasons (spring and summer–autumn) using variables similar to those already identified as important to bears (Mace et al. 1996, 1999; Boyce and Waller 2000). To adjust for autocorrelation and pseudo-replication, we use variance inflation factors (individual-level) and conditional fixed-effects logistic regression (population-level). We compare seasonal models to understand inter-seasonal dynamics and contrast these RSF models with habitat index models developed previously for the site.

STUDY AREA

The study was located along the eastern slopes of the Canadian Rocky Mountains in west-central Alberta's Yellowhead Ecosystem (Fig. 1). A number of studies on grizzly bears have been completed within or near this area (Pearson and Nolan 1976, Russell et al. 1979, Nagy et al. 1989, Kansas and Riddell 1995). The 5,352-km^2 study area was bordered by the Athabasca and Brazeau River in the north and south, a series of mountain ranges in the west, and a forestry trunk road to the east. Approximately half of the study area is protected as Jasper National Park (JNP, 43%) and Whitehorse Wildlands Provincial Park

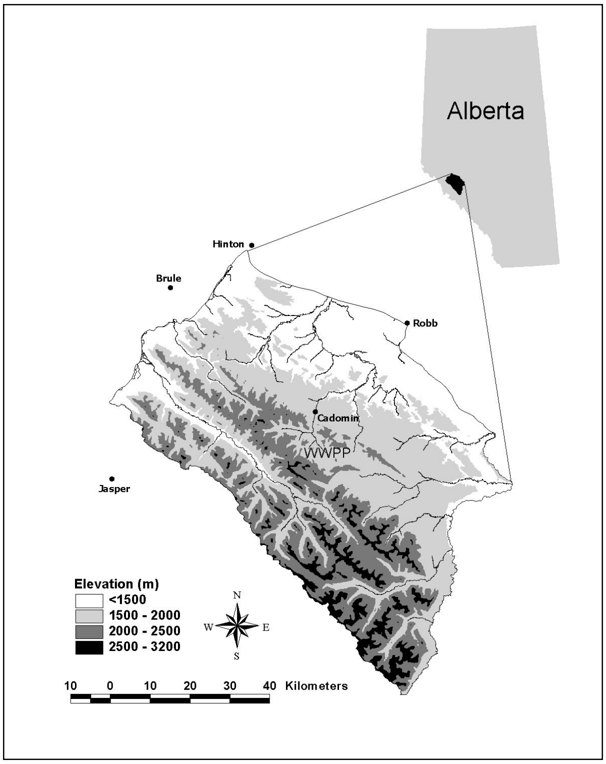

Fig. 1. Map of the 1999 study area within the Yellowhead Ecosystem of west-central Alberta, showing towns, principle rivers, elevation classes, study boundaries, and Whitehorse Wildlands Provincial Park (WWPP).

(WWPP, 3%). Elevations vary from 984 to 3,012 m. This topographic gradient generates a diverse pattern of habitats and ecosystems, delineated primarily by elevation and distance east from the Front Ranges (increasing boreal influence).

METHODS

Grizzly Bear Location Data

In 1999, we captured 23 adult (≥5-years old) and subadult (3–5 years old) grizzly bears using aerial darting and leg snaring techniques. Nineteen bears were fitted with either a Televilt (Lindesburg, Sweden) GPS (global positioning system)-Simplex radiocollar or an ATS (Advanced Telemetry Systems, Isanti, Minnesota,) GPS radiocollar. Radiocollars were programmed for 4-hr fix intervals. Following retrieval of collars, 6,057 locations were recovered from 14 bears (9 female and 5 male). Most locations (91%) were from 9 individual bears. We focused our analyses on these 9 individuals. For each, we obtained ≥346 locations over ≥100 days (Table 1). Locations were imported into a GIS (geographical information system) and used to delineate 100% minimum home range convex polygons (MCP; Samuel and Fuller 1994). Data were separated into 2 seasons. The first season, spring, was defined as the period between den emergence and 31 July. During this period, bears typically fed on roots of *Hedysarum* spp., horsetail (*Equisetum* spp.), and monocots (grasses and sedges) (Nagy et al. 1989). The second season, summer–autumn, was defined as 1 August–denning, during which bears entered hyperphagia and readily searched out berries from Canadian buffalo-berry (*Shepherdia canadensis*) and blueberries (*Vaccinium* spp.) (Nagy et al. 1989). Cumulative non-overlapping 100% MCP home ranges defined the population-level study area, while individual 100% MCP home range areas constrained the available resources for models of individual bears (Table 1).

Study Design

We evaluated third-order (Johnson 1980) seasonal resource selection. Resources were derived from remote sensing and GIS databases. Resource use, estimated from telemetry locations, was compared to resources at randomly sampled locations using logistic regression (Manly et al. 1993, Boyce and McDonald 1999). We define availability as all areas within 100% annual MCP home ranges. To characterize availability, we randomly generated 1,000 points within each animal's home range using a GIS. Coefficients from logistic regression analyses were used to estimate resource selection functions (RSF) by season for

Table 1. Identification, sex, age, radio-telemetry sample sizes by season, and 100% minimum convex polygon home range sizes used for resource selection function (RSF) analyses of grizzly bears in the Yellowhead Ecosystem, Alberta, 1999.

			GPS radio-telemetry locations			
Bear ID	Sex	Age	Spring	Summer–autumn	Annual	Home range size (km^2)
G2	F	17	321	150	471	662
G3	F	5	392	227	619	383
G4	F	5	406	388	794	460
G5	M	11	384	98	482	1298
G6	M	16	267	79	346	993
G8	M	14	305	89	394	1588
G10	F	13	334	149	483	482
G16	F	4	255	441	696	511
G20	F	4	190	494	684	718
All Bears			2,854	2,115	4,969	

both individual bears and the population.

Remote Sensing and GIS Data

Cover Type.—An integrated decision tree approach (IDTA) habitat classification was generated using a September 1999 Landsat TM satellite image (Franklin et al. 2001), a digital elevation model (DEM), a GIS vegetation inventory layer, and 320 field sites (Franklin et al. 2001). Twenty vegetation classes were generated with an overall habitat class accuracy of 83%. These 20 classes were combined into 8 major habitat classes (Table 2). Three additional classes were characterized from existing GIS maps. A forest management map of cut-block history was used to stratify stands into 13–22 year-old and 23–44 year-old cover classes. Fire history maps were used to classify young regenerating burn stands, which we considered to be all fire-regenerated stands >2 and <44 years of age. Prior to 1956, there was an inactive period of fires within the study area providing a convenient date for separating young regenerating forests from mature stands.

Greenness.—A tasselled-cap transformation of the September 1999 Landsat TM image was used to calculate greenness values across the study area (Crist and Cicone 1984, Manley et al. 1992). Greenness scores were divided into 10 classes similar to those used by Mace et al. (1999). High greenness values typically indicated areas of high vegetative reflectance and leaf area index (LAI), and low values indicated non-vegetated areas of rock, snow, and ice (White et al. 1997, Waring and Running 1998).

Streams.—Distance to 3 types of streams (major, perennial, and intermittent) was evaluated. Major streams were defined as hydrographic features that averaged ≥20 m between banks and were hydrologically active year round. Perennial streams were identified as hydrographic features with shorelines <20 m in width and continually flowing, except in drought conditions. Intermittent streams were hydrographic features averaging <20 m in width and often dry or obscured by vegetation during photo interpretation.

Table 2. Integrated decision tree approach (IDTA) habitat cover types generated for the study area using 1999 Landsat TM imagery (Franklin et al. 2001). Habitat classes were modified for resource selection function modeling.

Modified classes	Original IDTA map classes
closed forest	closed conifer closed deciduous mixed forest
open forest	open conifer open deciduous
alpine	alpine > 1800 m
herbaceous	Herbaceous < 1800 m herbaceous reclamation
shrub–wetland < 1800 m	shrub < 1800 m wetland-open bog wetland-treed bog
non-vegetated	rock snow shadow water road/rail line urban
cut 0–12-years old	recent cut (0–2-years old) cut 3–12-years old
recent burn	recent burn

Elevation and Hillshade.—We used a 100-m DEM to determine elevation for each location. We further used a quadratic term for elevation, since *a priori* we suspected non-linear selection of elevation zones (Waller and Mace 1997). A hillshaded grid model was derived from the DEM using the Spatial Analyst extension in ArcView 3.2 (ESRI, Redlands, California, USA). Aspect and slope were set within the hillshade model at 225° and 45°, respectively. High hillshade values corresponded to xeric southwest slopes, while low hillshade values depicted cool, mesic northeast slopes.

Access Density.—Linear features that could provide human access were placed into 3 categories (low, moderate, and high) based on potential impacts to bears, travel volume, and other characteristics. High-impact features included undivided paved and 2-lane gravel roads. Moderate-impact features included 1-lane gravel roads, unimproved roads, and truck trails. Low-impact features included seismic lines and utility lines (pipelines and transmission lines). The density of these features (km/km^2) was calculated within 9-km^2 moving windows around each 50-m grid pixel. Previous work identified 9 km^2 as the daily area used by adult female grizzly bears in the area (Gibeau 2000, Stenhouse and Munro 2000).

Modeling Procedures: Individual-Based RSF Models

Model Estimation and Structure.—We divided data from each season and grizzly bear into 2 groups following a *k*-fold partitioning design (Fielding and Bell 1997). The first group, the model-training data, represented a random 90% sub-sample of the telemetry and availability point data. The remaining 10% was used to assess model fit (model-testing) (Hosmer and Lemeshow 1989). Using the model-training data, we developed RSF models with the structure

$$w(x) = \exp\left(\beta_1 x_1 + \beta_2 x_2 + \ldots \beta_{20} x_{20}\right) \qquad (1)$$

where $w(x)$ is the resource selection function and b_i are selection coefficients based on environmental variables x_i (Manly et al. 1993). We used logistic regression in the program STATA (2001) to estimate the coefficients for each of the 20 explanatory variables described above by grizzly bear and season (i.e., 18 models). For the categorical cover class variable (11 habitat types), we used the most common habitat, closed forest, for reference. All estimated habitat coefficients are in reference to this class. We did not employ parsimonious model building strategies (Burnham and Anderson 1998), opting instead for full model designs where examinations of the patterns and significance of coefficients between models are possible (Hosmer and Lemeshow 1989). We excluded variables that were highly correlated ($r > 0.7$), because logistic regression is sensitive to colinearities among the explanatory variables (Hosmer and Lemeshow 1989). High correlations occurred only between high and moderate-impact access features. In such cases, we selected the high-impact access variable and removed the moderate-impact access variable.

Accounting for Autocorrelation.—Standard errors and associated significance levels were estimated using the Newey-West (Newey and West 1987) estimator of variance within a binomial logit generalized linear model (GLM) (McCullagh and Nelder 1989). This sandwich variance estimator accounts for autocorrelation between observations (dependent variable; see Lennon 1999) by inflating estimated standard errors. Estimates of the coefficients themselves are unaffected by autocorrelation and therefore equivalent between logistic regression models and GLM Newey-West estimates. For a purely predictive model, it may not matter whether observations were autocorrelated. However, because we were interested in the significance and corresponding inferences of the explanatory variables, adjustments were crucial. One would detect significance more frequently than one should (Type I error) without such adjustments (Lennon 2000). We determined the autocorrelation structure within our dependent variable (using residuals from initial individual-level logistic models) using partial autocorrelation functions. From these examinations, we found evidence of temporal autocorrelation occurring out to 3 to 6 distance lags (12–24 hours), depending on the bear. Based on these results and general biological considerations, we used a truncation lag of 6 observations for Newey-West variance estimation. This lag represented a 24-hour period where autocorrelation was considered significant and therefore in need of consideration and variance correction.

Model Building and Testing.—After initial full models were developed, outliers were detected using Pregibon's (1981) $\Delta\hat{\beta}$ influence statistic and the Hosmer and Lemeshow (1980) $\Delta\chi^2$ influence statistic (Lemeshow and Hosmer 1982). The $\Delta\hat{\beta}$ influence statistic measures the difference in the coefficient vector due to the deletion of each covariate, while the $\Delta\chi^2$ influence statistic measures the decrease in the Pearson χ^2 goodness-of-fit statistic from the deletion of subsequent observations. We plotted these 2 influence statistics together to detect and remove observations that excessively and negatively influenced model fit and coefficient estimation (Hosmer and Lemeshow 1989). Models were tested for overall fit using a Hosmer and Lemeshow (1989) goodness-of-fit statistic, $\hat{C}$, on both the training and testing datasets.

Modeling Procedures: Grizzly Bear Population-level RSF Models

We developed grizzly bear RSF models by season for the population of sampled bears. We examined the significance of explanatory variables used in the seasonal population-level models, the dynamics of selection between the seasons, and the difference between individual-averaged models and population-level RSF models. We also compared RSF models to habitat index models developed for the Cheviott mine proposal (BIOS 1996). To compare habitat index and RSF models, we generated a single parameter RSF model for each season using the habitat quality index values (0–5 rankings) associated with our use and random locations. Hosmer and Lemeshow goodness-of-fit values were examined between models for fit. To overcome problems of pseudo-replication (Hurlbert 1984, Otis and White 1999) and unequal sample sizes among bears, we used a robust clustering technique that imitates conditional fixed-effects logistic regression models (Pendergast et al. 1996). We therefore assumed independence between bears (clusters), but not necessarily between sub-samples (GPS locations). Without these corrections, parameter estimates as well as significance levels can be biased, potentially leading to inappropriate and misleading inferences. We followed similar model building and testing procedures at the population-level.

RESULTS

Individual-level RSF Models

Spring RSF Models.—RSF models for the spring season varied among individual bears with respect to significance of parameter estimates and goodness-of-fit tests (Table 3). Although models for all bears were significant over the null model, diagnostic tests suggested that some bears fit poorly to the training data (G2, G10, G20) and testing data (G4, G5, G10). The variability among individuals made generalizing resource selection difficult. However, during the spring season, most bears selected for areas of high greenness (5 of 9), distance to stream (4 of 9), and alpine areas (4 of 9; Table 4). Avoidance was evident for non-vegetated areas (6 of 9) and young regenerating forests (4 of 9). The influence of forest management cut blocks also varied considerably among individuals. Two bears (G5, G8) avoided cut-blocks of all age classes, but only recent cut-block avoidance by

Table 3. Model deviance, significance, goodness-of-fit, and validation for spring and summer–autumn resource selection function (RSF) models for grizzly bears in the Yellowhead Ecosystem, Alberta, Canada, 1999.

Season / Test	Grizzly bear number								
	G2	G3	G4	G5	G6	G8	G10	G16	G20
Spring									
Log likelihood									
Null model (-2LL)	658.0	739.6	756.3	720.2	575.9	634.4	672.0	563.0	457.3
Full model (-2LL)	549.4	626.4	626.9	493.2	439.7	578.4	542.8	464.1	366.2
pseudo-r^2	0.17	0.15	0.17	0.32	0.24	0.09	0.19	0.18	0.20
Model significance									
Model χ^2, df	217.2, 12	216.1, 12	258.9, 14	453.9, 19	272.4, 13	112.0, 18	258.5, 12	197.7, 14	182.1, 19
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Model training: Goodness-of-fit $\hat{C}$									
(8 df)	19.28	8.89	8.52	12.98	7.92	4.79	15.41	4.39	15.73
P	0.013	0.352	0.384	0.113	0.442	0.780	0.052	0.820	0.046
Model testing: Goodness-of-fit $\hat{C}$									
(8 df)	11.59	7.48	36.52	17.87	6.28	8.74	14.20	12.23	6.01
P	0.170	0.486	<0.001	0.022	0.616	0.365	0.077	0.141	0.646
Summer–autumn									
Log likelihood									
Null model (-2LL)	386.3	516.8	736.1	272.9	240.8	250.1	394.6	795.3	851.2
Full model (-2LL)	326.3	387.8	452.0	214.4	137.6	174.6	243.1	581.8	586.3
pseudo-r^2	0.16	0.25	0.39	0.21	0.43	0.30	0.38	0.27	0.31
Model significance									
Model χ^2, df	120.2, 12	258.0, 11	568.2, 14	117.0, 17	206.4, 12	150.8, 14	303.1, 12	426.9, 14	529.7, 20
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Model training: goodness-of-fit $\hat{C}$									
(8 df)	19.78	12.58	37.10	12.74	24.76	7.11	17.93	8.02	11.84
P	0.011	0.127	<0.001	0.121	0.002	0.515	0.022	0.432	0.158
Model testing: goodness-of-fit $\hat{C}$									
(8 df)	11.87	15.51	17.54	36.02	5.28	447.71	5.10	235.26	3.61
P	0.157	0.050	0.025	0.000	0.728	<0.001	0.747	<0.001	0.890

G5 was significant. Bear G20 selected for both mid-aged (13–22 yr old) and older (22–44 yr old) cut-blocks. Bear G20 was also found to occur in areas associated with high levels of both high and low-impact access features, relative to that which was available. Conversely, G16 avoided habitats with high levels of high and low-impact access features.

Summer–autumn RSF Models.—RSF models for the summer–autumn season again varied substantially among individual bears (Table 3). However, most summer–autumn models did fit and explained deviance better than spring models. All models were significant over null models. Goodness-of-fit diagnostics suggested poor fit for 4 bears (G2, G4, G6, G10) using training data and 5 bears (G3, G4, G5, G8, G16) using testing data. Variability of estimated selection coefficients was again observed among individuals during the summer–autumn season (Table 5). However, the importance of greenness for predicting bears during this season was evident for all individual models. Eight bears demonstrated selection for areas of high greenness, while 1 bear (G2) demonstrated avoidance. IDTA habitat classes significantly contributed to the prediction of individual bears. Alpine (4 of 9) and shrub–wetland (3 of 9) classes maintained the most consistency for selected habitats. Regenerating burns (4 of 4) and non-vegetated (5 of 9) classes were consistently avoided. Selection for streamside habitats continued to be common (8 of 9) through the summer–autumn season. Bear G20 continued to associate with high-density areas of both high and low-impact access features, and G8 selected for areas with moderate-impact features. Four bears (G4, G6, G8, G16) avoided habitats with high-impact features. Selection and avoidance of low-impact features was variable depending on bear.

Inter-seasonal Dynamics.—In comparing individual grizzly bear models between seasons, a number of inter-seasonal selection coefficients were significantly different (non-overlapping 95% Newey-West confidence intervals). Cut blocks 13–22 years of age were selected during the spring by G20 but avoided during the summer–autumn season. Bear G20 also showed strong selection for areas of high greenness during summer–autumn, but no such selection in the spring. Two bears, G10 and G5, selected for areas near intermittent and perennial streams during the spring but either avoided (G10) or used as available (G5) during the summer–autumn. Bears G4 and G8 avoided high-impact access features in the spring but not during summer–autumn. Bears G2, G3, G6, and

Table 4. Estimated coefficients by bear for spring resource selection function models (RSF). Significance of parameters was determined using Newey-West sandwich variance estimators with a correlation lag distance of 6. Missing estimates for habitat features represent habitat not represented within home range (MCP) of animal.

	Grizzly bear									
Variable	G2	G3	G4	G5	G6	G8	G10	G16	G20	Average[a]
Habitat class										
Alpine	0.447	-0.243	0.398	0.053	0.444	0.701[b]	0.665[b]	0.433	0.210	0.345
Recent burn				-0.328					1.837[b]	0.754
Cut 0–12 yr				avoid[c]		-0.475			0.171	-0.152
Cut 13–22 yr				-0.338		-0.053			0.940[b]	0.183
Cut >22 yr				-0.437		-0.377			0.557[b]	-0.085
Herbaceous		select[c]	0.232	-0.327	avoid[c]	0.370	-0.446	0.539	1.021[b]	0.232
Open forest	0.025	-0.176	0.454[b]	0.319	0.460	0.195	0.047	-0.070	0.070	0.147
Non-vegetated	-0.163	-0.587[b]	-0.765[b]	-0.280	-0.257	-1.032[b]	-0.727[b]	-0.169	0.032	-0.439
Regen. burn				-1.092[b]		avoid[c]			avoid[c]	-1.092
Shrub–wetland	0.749	0.837	-0.139	0.541[b]	0.960[b]	-0.181	1.100[b]	0.062	1.256[b]	0.576
Habitat features										
Greenness	0.159	0.412[b]	0.212[b]	0.121	0.489[b]	0.176	0.450[b]	0.315[b]	0.068	0.267
Major streams[d]	-0.121	0.089	0.244[b]	-0.251[b]	0.162[b]	0.058	0.059	-0.286[b]	-0.145[b]	-0.021
Perennial streams[d]	-0.135	0.172	-0.148	-0.820[b]	-0.897[b]	-0.087	0.116	-0.400[b]	-0.247[b]	-0.272
Intermittent streams[d]	-0.250[b]	-1.344[b]	-0.417	0.031	0.049	-1.555[b]	0.229	-0.879	-0.762	-0.544
Hillshade	0.008[b]	-0.008[b]	0.010[b]	0.004	0.003	-0.003	0.009[b]	-0.011[b]	0.004	0.002
Elevation	0.025[b]	0.062[b]	0.034[b]	0.090[b]	0.026[b]	-0.001	0.022	0.083[b]	0.027[b]	0.041
Elevation^{2} [e]	-0.514	-1.540[b]	-0.094[b]	-0.297[b]	-0.692[b]	-0.020	-0.639[b]	-2.210[b]	-0.657[b]	-0.740
Access density										
High			-0.185	-0.222	-0.315	2.224[b]		-2.724[b]	2.060[b]	0.140
Moderate				0.581[b]		-0.405			0.521	0.232

[a] Averages include only parameters that have been estimated
[b] $P < 0.10$
[c] Perfect avoidance or selection; parameter estimate not available (approaches infinity)
[d] Estimated β for distances to streams measured in kilometers (negative coefficient represents selection)
[e] Estimated β for elevations measured in 100-km units

G16 failed to show significant inter-seasonal dynamics at the seasonal scale we examined.

Population-level RSF Models

Spring RSF Model.—Overall, the spring RSF model was significant (-2LL = 5420.4, χ^2 = 917.6, 20 df, P < 0.001, r^2 = 0.08). Goodness-of-fit tests further confirmed fit between model training data ($\hat{C}$ = 8.27, 8 df, P = 0.408) and testing data ($\hat{C}$ = 10.76, 8 df, P = 0.215; Table 6). Maps showed relative probabilities of use for some areas (e.g., WWPP) as high, while areas of low use included the horseshoe-shaped 1956 burn (Fig. 2).

Explanatory variables contributing significantly (P < 0.1) to the overall model following adjustment for individual bear (Table 6; note the detection of significance [Type I error] for 9 additional parameters without adjustment) included alpine, non-vegetated habitats, regenerating burns, greenness, and perennial streams. Grizzly bears selected for areas of high greenness. Perennial streams were selected, while both major streams and intermittent streams were used in proportion to their availability. Alpine habitats were selected, while both non-vegetated areas and young (3–44 year old) regenerating burns were strongly avoided when compared to the reference category of closed forest stands. Grizzly bears were 8 times less likely to be present in regenerating burns than closed conifer forests. No significant patterns were detected for cut blocks, although there was a tendency for recent cut block classes (0–12 years old) to be avoided. Access density, elevation and hillshade all failed to affect distributions of grizzly bears during the spring season.

Summer–Autumn RSF Model.—Overall, the summer–autumn RSF model was significant (-2LL = 4110.0, χ^2 = 1493.7, 20 df, P < 0.001, r^2 = 0.15). Hosmer-Lemeshow χ^2 goodness-of-fit tests showed evidence of poor model fit for training data ($\hat{C}$ = 35.46, 8 df, P <0.001), but reasonable fit for testing data ($\hat{C}$ = 10.76, 8 df, P = 0.215). Maps illustrated a heterogeneous structure to the landscape with small areas showing well-differentiated relative probability of use occurring in the mountains of JNP along high alpine bowls (Fig. 3).

Explanatory variables that contributed significantly to the model included alpine, recent burn, cut blocks 22–44 years of age, open forest, regenerating burn, shrub–wetlands, greenness, rivers, perennial streams, and both high- and moderate-impact access density. High values of greenness were again strong predictors of grizzly bear occurrence. Bears also tended to be found along major streams, with only a slight preference for habitats along perennial streams. Habitat classes where significant selection occurred included alpine habitats, recently burned stands, cut blocks 22–44 years of age, herbaceous areas, open

Table 5. Estimated coefficients by bear for summer–autumn resource selection function (RSF) models. Significance of parameters was determined using Newey-West sandwich variance estimators with a correlation lag distance of 6. Missing estimates for habitat features represent habitat not represented within home range (MCP) of animal.

	Grizzly bear									
Variable	G2	G3	G4	G5	G6	G8	G10	G16	G20	Average[a]
Habitat class										
Alpine	0.455	0.143	0.839[b]	0.822	-0.084	2.095[b]	1.003[b]	1.337[b]	0.198	0.757
Recent burn			avoid[c]	avoid[c]					0.302	0.302
Cut 0–12 yr				0.082		avoid[c]			0.164	0.123
Cut 13–22 yr				avoid[c]		-0.405			-1.318[b]	-0.862
Cut >22 yr				-0.135		avoid[c]			-0.268	-0.201
Herbaceous			0.581	-0.699	-0.394	avoid[c]	-0.727	1.516	0.866[b]	0.191
Open forest	-0.435	0.482	0.263	-1.436[b]	0.166	0.252	0.151	0.628[b]	0.743	0.090
Non-vegetated	-1.119[b]	-1.447[b]	-1.009[a]	0.596	-1.752[b]	avoid[c]	-0.844	0.012	0.607[b]	-0.619
Regen. burn			avoid[c]	avoid[c]		avoid[c]			-1.804[b]	-1.804
Shrub–wetland	0.230	avoid[c]	-0.239	0.295	3.360[b]	-0.056	0.555	1.418[b]	0.874[b]	0.805
Habitat features										
Greenness	-0.293[b]	0.244[b]	0.319[b]	0.445[b]	0.553[b]	0.641[b]	0.647[b]	0.262[b]	0.575[b]	0.377
Major Streams[d]	-0.271[b]	-0.004	-0.239[b]	-0.262[b]	0.035	-0.137	-0.084	-0.256[b]	-0.457[b]	-0.186
Perrenial Streams[d]	-0.556[b]	0.700	-0.875[b]	-0.022	-1.273	-0.418[b]	-1.800[b]	-0.184	-0.071	-0.500
Intermittent Streams[d]	-0.247[b]	-1.102[b]	-0.483	1.960[b]	0.488[b]	-1.200	0.243[b]	-2.738[b]	0.085	-0.333
Hillshade	0.014[b]	-0.001[b]	0.003	-0.005	0.010[b]	-0.018[b]	0.000	0.006[b]	-0.010[b]	0.000
Elevation	0.028	0.015[b]	0.019	0.011[b]	0.159[b]	0.042[b]	0.050[b]	0.070[b]	-0.014[b]	0.042
Elevation^2 [e]	-0.684	-0.287[b]	-0.548	-0.288	-4.050[b]	-1.100[b]	-1.380[b]	-1.860[b]	0.521[b]	-1.075
Access density										
High			-4.961[b]	-0.783	avoid[c]	-5.404[b]		-8.122[b]	1.841[b]	-3.486
Moderate				-0.560		4.037[b]			0.159	1.212
Low	-5.058[b]	-2.401[b]	-1.164[b]	0.691[b]	select[c]	-0.141		-0.263[b]	0.206[b]	-1.161
# Significant	7	8	9	9	9	13	6	11	12	

[a] Averages include only parameters that have been estimated
[b] $P < 0.10$
[c] Perfect avoidance or selection; parameter estimate not available (approaches infinity)
[d] Estimated β for distances to streams measured in kilometers (negative coefficient represents selection)
[e] Estimated β for elevations measured in 100-km units

forests, and shrub–wetland habitats. Young regenerating forest burn stands were strongly avoided. Bears tended to use areas of high-impact access density, although this appears to be mostly due to selections made by 2 bears, G20 and G5. The reverse relationship occurred for moderate-impact access density areas, as bears tended to avoid truck trails, unimproved roads, and 1-lane gravel roads. Intermittent streams, hillshade, and elevation did not significantly contribute to explaining patterns of use during the summer–autumn season.

Inter-seasonal Dynamics.—Model parameters that differed between seasons (based on non-overlapping 95% confidence intervals) included alpine habitats and moderate-impact access density. Selection of alpine habitats, significant for both seasonal models, increased substantially between the spring and summer–autumn period, with the (odds ratio) likelihood of use more than doubling from 1.5 to 3.4. Moderate-impact access density was non-significant during the spring season but strongly significant and negative (indicating avoidance) during the summer–autumn season.

RSF Model vs. Habitat Index Model.—The spring habitat index RSF model was significant (-2LL = 5679.4, χ^2 = 52.73, 1 df, $P < 0.001$, $r^2 = 0.03$) overall, but failed to maintain fit in Hosmer-Lemeshow goodness-of-fit tests on both the training data ($\hat{C} = 64.3$, 6 df, $P \leq 0.001$) and testing data ($\hat{C} = 31.8$, 8 df, $P < 0.001$). The summer–autumn habitat index RSF model also was significant (-2LL = 4811.6, $\chi^2 = 5.9$, 1 df, $P = 0.015$, $r^2 = 0.01$) overall, but again failed to maintain fit in Hosmer-Lemeshow goodness-of-fit tests on training data ($\hat{C} = 527.9$, 4 df, $P < 0.001$) and testing data ($\hat{C} = 61.21$, 6 df, $P < 0.001$). Full RSF models and models using greenness alone increased fit over that of habitat index models.

DISCUSSION

Although adjusted for pseudo-replication and autocorrelation, inferences and interpretations of parameters still should be interpreted cautiously because non-random errors likely were present in GPS collar data (Obbard et al. 1998, Dussault et al. 1999, Rettie and McLoughlin 1999). Promising new methods are currently becoming available that directly incorporate GPS collar bias within RSF models (J.L. Frair et al., University of Alberta, Alberta, Canada, unpublished data).

Although grizzly bears likely select resources at different spatio-temporal scales, selection for resources at the

Table 6. Variables, parameters, model fit, and model validation of seasonal RSF grizzly bear models for the Yellowhead Ecosystem, Alberta, Canada based on 1999 data. Individual-based average coefficient estimates (I-Model, mean b_i average) are provided for comparison. Model fit evaluated with log likelihood (-2LL) statistics and goodness-of-fit tests (β).

	Spring				Summer–autumn			
Variable	β_i	Robust SE	P	I-Model Mean β_i	β_i	Robust SE	P	I-Model Mean β_i
Habitat class								
Alpine	0.433	0.132	0.001	0.345	1.227	0.245	<0.001	0.757
Recent burn	0.638	0.584	0.275[a]	0.754	0.691	0.328	0.035	0.302
Cut 0–12 yr	-1.651	1.039	0.112[a]	-0.152	-0.091	0.270	0.735	0.123
Cut 13–22 yr	0.130	0.317	0.682	0.183	-0.518	0.319	0.105[a]	-0.862
Cut >22 yr	-0.118	0.272	0.664	-0.085	0.632	0.344	0.066	-0.201[b]
Herbaceous	0.232	0.231	0.316	0.232	0.839	0.338	0.013	0.191
Open forest	0.168	0.148	0.257[a]	0.147	0.519	0.143	<0.001	0.090[b]
Non-vegetated	-0.354	0.060	<0.001	-0.439	0.047	0.201	0.816	-0.619[b]
Regenerating burn	-2.092	0.485	<0.001	-1.092[b]	-1.856	0.309	<0.001	-1.804
Shrub–wetland	0.329	0.207	0.112[a]	0.576	0.365	0.187	0.051	0.805[b]
Habitat features								
Greenness	0.286	0.041	<0.001	0.267	0.384	0.045	<0.001	0.377
Major streams[c]	0.020	0.049	0.688	-0.021	-0.157	0.047	0.001	-0.186
Perennial streams[c]	-0.242	0.110	0.028	-0.272	-0.177	0.107	0.097	-0.500[b]
Intermittent streams[c]	0.032	0.083	0.700	-0.544[b]	-0.117	0.110	0.289[a]	-0.333
Hillshade	0.001	0.003	0.638[a]	0.002	0.002	0.002	0.274[a]	0.000
Elevation	0.005	0.006	0.387[a]	0.041[b]	-0.0001	0.004	0.983	0.042[b]
Elevation^{2} [d]	-0.135	0.172	0.434[a]	-1.13	-0.022	0.146	0.880	-1.08
Access density								
High	0.730	0.462	0.114[a]	0.140	1.456	0.574	0.011	-3.486[b]
Moderate	0.027	0.468	0.954	0.232	-1.403	0.543	0.010	1.212[b]
Low	0.063	0.111	0.569[a]	-0.017	-0.095	0.130	0.464[a]	-1.161[b]
Log likelihood								
Null model (-2LL)		5879.2				4856.8		
Full model (-2LL)		5420.4				4110.0		
Pseudo-r^2		0.08				0.15		
Goodness-of-fit $\hat{C}$								
Model training $\hat{C}$ (8 df)		8.27				35.50		
Model training P		0.408				<0.001		
Model testing $\hat{C}$ (8 df)		10.76				9.59		
Model testing P		0.215				0.477		

[a] Indicates significance ($P < 0.10$) of parameters from non-adjusted model estimation (standard logistic regression), but non-significance following robust clustering adjustments (variance inflation).
[b] Indicates that estimated average coefficients from individual-based models are significantly different from population-level estimates (based on 95% C.I.; averages include only parameters that have been estimated).
[c] Estimated β for distances to streams measured in kilometers (negative coefficient represents selection).
[d] Estimated β for elevations measured in 100-km units.

third order (patch-level) level is an important scale for predicting and understanding seasonal animal occurrences. It is also at this scale (stand-level) that land management decisions are frequently made. Predictive maps of habitat quality at the population-level can assist decision-making and conservation-planning efforts. RSF models can also be used to link habitats to population numbers (Boyce and McDonald 1999), providing an approach to habitat-based population viability analyses (see Boyce et al. 2001).

Our individual-based RSF models revealed a high degree of variability in selection of resources. Although using the average coefficients from multiple individuals may seem to be an appropriate method for determining population-level responses, our population-level models indicated that biases are likely using this approach. High variability among individual grizzly bears reduced the predictive power of population-level models. One potential solution might be to stratify individuals into similar groups and then develop separate population models. An alternative approach would be to understand functional responses of individual selection coefficients to availability of resources (Mysterud and Ims 1998). Differences in inter-seasonal selection were observed for only 2 variables at the population-level: alpine habitats and habitats associated with moderate-impact access density features. Selection behaviors during the spring season were substantially less predictable than summer–autumn models. Because these models were developed from only one year of data (1999), changes in coefficients are likely between years because long-term patterns may differ due to weather or other factors.

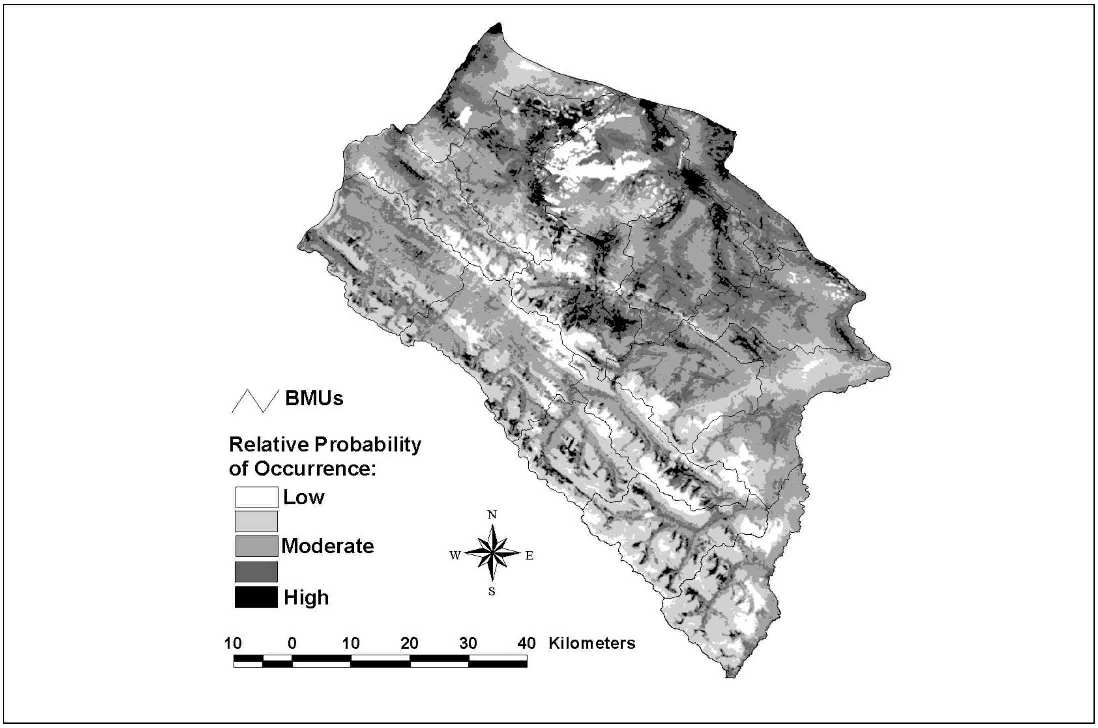

Fig. 2. Relative probability of use for Yellowhead grizzly bears during the spring season, based on 1999 data from Yellowhead Ecosystem, Alberta, Canada. This model is based on GIS layers and resource selection function model parameters at the level of the population. Bear management units (BMU) lines are displayed for reference.

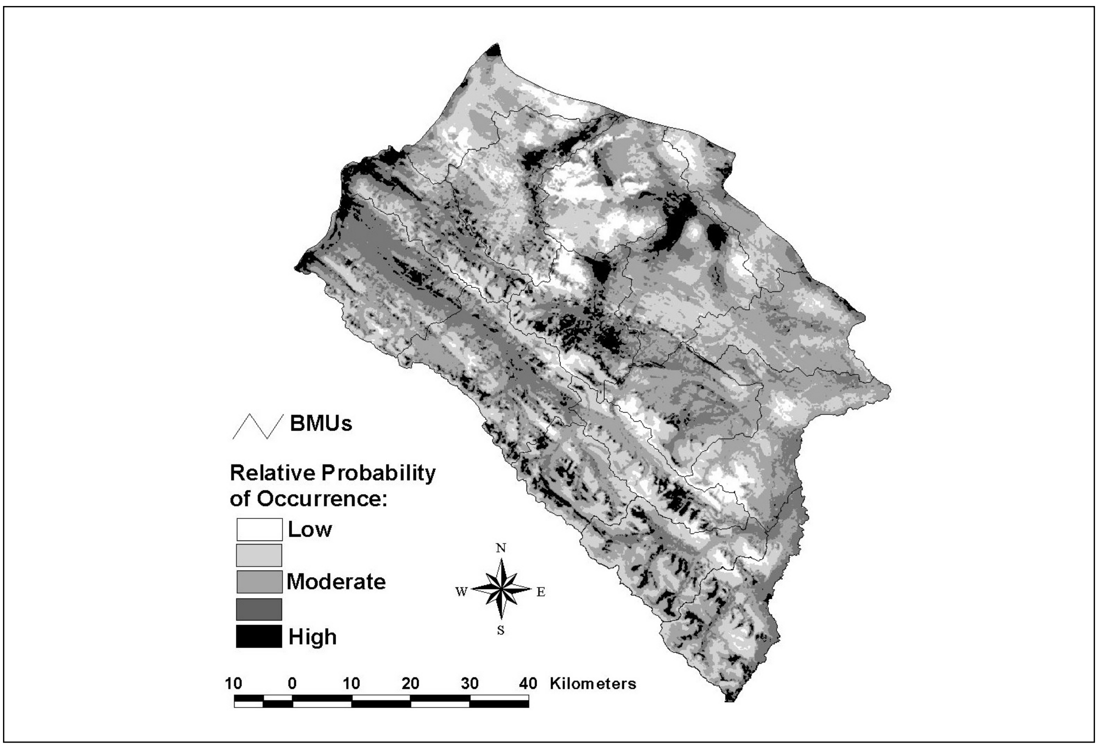

Fig. 3. Relative probability of use for Yellowhead grizzly bears during the summer–autumn season based on 1999 data from Yellowhead Ecosystem, Alberta, Canada. Model is based on GIS layers and resource selection function (RSF) model parameters at the level of the population. Bear management units (BMU) lines are displayed for reference.

Over-estimation of model fit was evident for training set models when compared to our independent *k*-partitioned testing data. Although rarely done, assessment of the RSF model through independent out-of-sample or in-sample data sources is essential for validating the applicability and robustness of models (Boyce et al. 2002). Significance levels for variables were over-estimated in unadjusted logistic regression models. Without careful adjustments, biases may exist in the interpretation and inference of model parameters.

Existing seasonal habitat index models for grizzly bears in Alberta are questionable for their use in predicting bear occurrence. Models using these habitat indices performed poorly, although full RSF models and models using greenness alone (not reported in detail here) substantially improved fit. Perhaps the most important predictor of bear occurrence was the Landsat TM greenness index. Consistency across ecosystems for this habitat quality surrogate pointed to its potential application for multi-ecosystem scale grizzly bear habitat modeling, where time and cost may limit conservation mapping exercises (Mace et al. 1999). Terrain variables frequently used in predicting animal occurrences and the distribution of food items (e.g., Nielsen and Haney 1998) were not found useful at the level of the population. All models indicated that old natural disturbances (regenerating burn 3–44 years old) were consistently strongly avoided. High levels of coarse woody debris in stands burned in 1956 likely has restricted movement and access for bears, while succeeding lodgepole pine (*Pinus contorta*) reduced light levels and food resources from initial high-levels observed in recently burned stands where bears have shown selection. Conversely, cut blocks were used past 12 years of age and avoided if younger. Access density also was an important variable; bears avoided moderate-impact access density features during summer–autumn. Movement rates tended to decrease substantially during this period (S.E. Nielsen, unpublished data), perhaps pointing to shorter or less frequent inter-patch movements or the concentration of feeding bouts within high-quality contiguous habitats.

Individual bears using habitats closely associated with roads and other linear disturbance networks (e.g., G20) face increased mortality risks (McLellan and Shackleton 1988, McLellan 1989, Nagy and Gunson 1990, McLellan et al. 1999). Currently, the foothills east of Jasper National Park contain high levels of linear access features, with average total density (low, moderate, and high-impact) at 2.11 km/km^2 (SD = 1.42). Understanding how development might affect grizzly bear population viability will be essential to resource planning on Alberta's east slopes.

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