

# Development and testing of phenologically driven grizzly bear habitat models<sup>1</sup>

Scott E. NIELSEN<sup>2</sup> & Mark S. BOYCE, Department of Biological Sciences, University of Alberta,

Edmonton, Alberta T6G 2E9, Canada, e-mail: scottn@ualberta.ca

Gordon B. STENHOUSE, Alberta Sustainable Resources Department, Fish and Wildlife Division,

Box 6330, Hinton, Alberta T7V 1X6, Canada.

Robin H. M. MUNRO, Foothills Model Forest, Box 6330, Hinton, Alberta T7V 1X6, Canada.

**Abstract:** We developed and compared three habitat models for estimating the relative probability of occurrence, by month, for grizzly bears (*Ursus arctos*) in Jasper National Park (JNP), Alberta. These models included 1) a habitat map derived from remote sensing Landsat imagery; 2) food-index models generated from the predicted occurrence of bear foods and assigned monthly importance values; and 3) probabilistic food models representing the occurrence of each bear food. Resource selection function (RSF) models for grizzly bears were generated using 3,924 global positioning system (GPS) radiotelemetry locations and the above habitat models. Comparisons were made among RSF models, by month, using Akaike's Information Criterion (AIC). In all seven months (April to October), food-index models performed poorly. In April and July, the remote-sensing habitat map predicted bears best, while the food-probability models performed best in the remaining five months. Overall, we found substantial improvement by using food-probability models for predicting JNP grizzly bear occurrence. Remote-sensing maps, although predictive, may not reveal underlying mechanisms and fail to recognize the dynamic nature of seasonal grizzly bear habitats. The disconnect between food-index and food-probability models suggests that monthly food importance values require additional parameterization. Development of spatial food models on phenologically important scales more closely matches the resources and temporal scales at which animals perceive and use resources.

**Keywords:** Alberta, grizzly bears (*Ursus arctos*), habitat selection, habitat modeling, Jasper National Park, phenology, resource selection functions (RSF).

**Résumé :** Nous avons développé et comparé trois modèles d'habitats dans le but d'estimer la probabilité relative de la présence, à chaque mois, d'ours grizzly (*Ursus arctos*) dans le parc national de Jasper en Alberta. Ces modèles comprennent : 1) une carte des habitats construite à partir des images satellitaires Landsat, 2) des modèles d'indices de nourriture (prédiction de la présence de nourriture associée à une valeur d'importance pour chaque mois) et 3) des modèles de nourriture probabilistes représentant la présence de chaque source de nourriture. Les modèles de fonction de sélection de ressources (FSR) pour les ours grizzly ont été établis à partir de 3924 localisations radiotéléométriques déterminées par système de positionnement géographique et à partir des modèles d'habitats décrits plus haut. Nous avons comparé les modèles FSR, par mois, en utilisant les critères d'information Akaike. Les modèles d'indices de nourriture n'ont pas donné de bons résultats quelque soit le mois considéré (avril à octobre). Pour les mois d'avril et de juillet, c'est la carte des images satellitaires qui a le mieux réussi à prédire la présence d'ours, alors que pour les cinq autres mois, les modèles de probabilité de nourriture ont donné les meilleurs résultats. En conclusion, l'utilisation de modèles de probabilité de nourriture apporte de nets avantages pour la prédiction de la présence des ours dans le parc national de Jasper. Les cartes d'images satellitaires, bien qu'elles soient d'une certaine utilité pour prédire la présence des ours, ne révèlent pas nécessairement les mécanismes sous-jacents et ne permettent pas de reconnaître la nature dynamique des habitats saisonniers de l'ours grizzly. L'absence de relation entre les modèles d'indices de nourriture et ceux de probabilité suggère qu'il serait préférable d'évaluer de nouveaux paramètres afin de mieux quantifier l'importance de la nourriture des ours pour chaque mois. Les modèles spatiaux de nourriture utilisant des échelles phénologiques appropriées se rapprochent beaucoup plus de la réalité perçue par les animaux lorsqu'il s'agit d'utiliser les ressources d'un territoire.

**Mots-clés :** Alberta, ours grizzly (*Ursus arctos*), sélection de l'habitat, modélisation de l'habitat, parc national de Jasper, phénologie, fonctions de sélection de ressources (FSR).

**Nomenclature:** Moss, 1994; Honacki, Kinman & Koepl, 1982.

## Introduction

Habitat loss threatens the persistence of grizzly bears (*Ursus arctos*) in the Rocky Mountains of Canada and the United States (Clark, Paquet & Curlee, 1996; McLellan & Banci, 1999). Identifying grizzly bear habitats is therefore important. Habitat models and maps are essential for conservation and management planning, cumulative effects assessments, and habitat-based population viability analyses

(Mladenoff *et al.*, 1995; Boyce & McDonald, 1999). Two principal approaches have been used for modeling grizzly bear habitats: 1) a bottom-up food approach (Kansas & Riddell, 1995; Mattson *et al.*, 1999; Mattson 2000); and 2) a top-down remote-sensing approach (Mace *et al.*, 1996; Mace *et al.*, 1999; Boyce & Waller, 2000; Nielsen *et al.*, 2002). Management of grizzly bears in the four contiguous mountain parks of Canada (Banff, Jasper, Kootenay, and Yoho) is based on a habitat-effectiveness model that uses the former method for classifying potential habitats (Gibeau,

<sup>1</sup>Rec. 2002-02-26; acc. 2002-08-26.

<sup>2</sup>Author for correspondence.

1998; Anonymous, 1998). Habitat quality for this model is based on the presence and abundance of 41 species of plant foods from field vegetation plots and monthly importance values within 135 ecological land survey vegetation types (Kansas & Riddell, 1995). Recently, Nielsen *et al.* (2002) found that such models predicted grizzly bear radiotelemetry occurrence in west-central Alberta poorly.

In contrast to this bottom-up approach, grizzly bear habitat models/maps have been developed for a number of areas, most notably that of northwest Montana (Mace *et al.*, 1996; Mace *et al.*, 1999), using remote-sensing data (vegetation classifications and habitat surrogates like greenness), animal radiotelemetry locations, and habitat selection modeling (Manly, McDonald & Thomas, 1993). This top-down approach relies on geographical information system (GIS) and remote-sensing data, which are readily available across large spatial extents. Such information, when related to animal locations, can be used to produce predictions of animal occurrence (*i.e.*, GIS maps), useful for addressing conservation questions. These habitat models, however, require large numbers of animal locations to train model estimates. Furthermore, there is no reason to believe that GIS and remote-sensing data are at the appropriate scale (spatial or temporal) at which animals select resources or even that such data are relevant (perceived) to the species (Lennon, 1999; Morrison, 2001). Researchers also often fail to recognize or are unable to examine (due to low sample sizes) phenological food seasons and therefore pool animal location data (Schooley, 1994). Given these limitations, mechanisms responsible for selection are not easily interpreted (Garshelis, 2000; Morrison, 2001). Comparisons and implications of using food and remote-sensing-based habitat models therefore need further examination.

In this paper, we develop and test the efficacy of food and remote-sensing models for predicting grizzly bear occurrence in Jasper National Park (JNP), Alberta. We compare food models developed from 32 species of plant foods to a more traditional habitat-relationship analysis that uses a remotely sensed habitat classification. We attempt to develop GIS models of direct resource gradients (food) perceived and used by local grizzly bear populations. Herein, we make four principal assumptions in the development and testing of food models for comparison with remote-sensing maps: 1) the most relevant factor influencing grizzly bear habitat selection is food; 2) the vast majority of a grizzly bear's nutritional demand in the northern Rockies is met through herbivorous feeding activities (Jacoby *et al.*, 1999); 3) presence/absence of foods is sufficient to predict grizzly bear occurrence, even though energetic or productivity characteristics may be more reasonable and/or predictive (Mattson *et al.*, 1999; Mattson, 2000); and 4) monthly time steps (scale at which importance values are available) are at a sufficient temporal scale to cover phenological developments and use of bear foods. Due to these assumptions and the possibility of habitat and terrain bias associated with global positioning system (GPS) radiotelemetry data (Dussault *et al.*, 1999), we consider this paper more a methodological test of the usefulness of different spatial data for predicting grizzly bear occurrence than a calculation of robust habitat coefficients used for management and conservation.

## Methods

### STUDY AREA

Our study was located in Jasper National Park (10,878 km<sup>2</sup>) in west-central Alberta, Canada (52° 50' N, 118° 00' W) in the Front Ranges of the Canadian Rocky Mountain Cordillera (Figure 1). Drainage pattern is influenced strongly by topography and runs predominately toward the Athabasca River, an Arctic watershed. Elevations vary from 953 m near the town site of Jasper to 3,581 m in the Columbia Icefield on the British Columbia-Alberta border. Alpine habitats typically begin at elevations ranging between 1,900 and 2,100 m, depending on soil moisture (hygric to xeric) and aspect (La Roi & Hnatiuk, 1980), while montane grasslands characteristically occur below 1,350 m in the Athabasca Valley (Holland & Coen, 1982). Situated between these two open communities are areas of forest, primarily composed of spruce (*Picea* spp.), fir (*Abies* spp.) and lodgepole pine (*Pinus contorta*). Substantial areas of rock and ice are found throughout the park, typically above 2,400 m in elevation.

### REMOTE SENSING HABITAT MAP

An Integrated Decision Tree (IDT) habitat classification was generated for an area of west-central Alberta using a September 1999 Landsat satellite image, a digital elevation model (DEM), GIS vegetation inventories, and field ground-truth sites (Franklin *et al.*, 2001). This 30-m-resolution map was produced for a grizzly bear study that covers a 2,300-km<sup>2</sup> area of JNP (Figure 1) and a large area of adjacent foothill habitats to the east. Using classified habitats from JNP, we reclassified the original map into five principal vegetative cover types common to the mountainous region of the study area. These cover types included alpine, closed forests, open conifer, shrub/wetland complexes, and non-vegetated habitats (*e.g.*, snow, rock, shadow, and water). An accuracy assessment found accuracy of the original IDT map classification to be 80.16% (Franklin *et al.*, 2001).

### FOOD-INDEX MODELS

We used 1,343 field vegetation plots established in 1977-1979 in JNP to predict bear plant foods used by grizzly

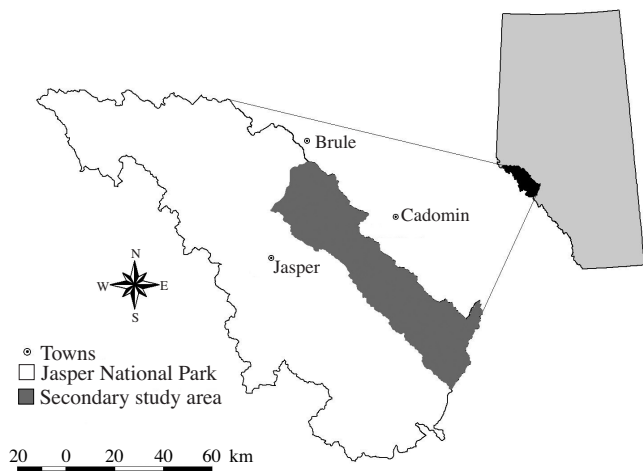


FIGURE 1. Map of Jasper National Park in western Alberta, showing principal towns, study boundary, and secondary study area where grizzly bear RSF models were tested.

bears. In total, we recognized 32 species of potential plant foods common to both JNP field data (prevalence > 5%) and local food habitats studies (Kansas & Riddell, 1995). Using logistic regression we developed predictive models for each species, with 11 covariates from the Yellowhead Ecosystem Working Group (YEWG) ecological land classification (Gordon *et al.*, 1998) and other existing GIS data (Table I; Figure 2). These data include terrain, habitat, soil, and disturbance history information. Elevation was estimated from a 100-m digital elevation model (DEM), while hillshade was estimated using the same DEM and the Spatial Analyst extension in ArcView. Aspect and maximum slope were set in the hillshade model to 225 and 45 degrees respectively, thus representing local terrain site moisture (*i.e.*, xeric [SW slopes] to mesic [NE slopes]) characteristics (Nielsen & Haney 1998; Nielsen *et al.*, 2002). Habitat variables included forest versus open sites and barren/unvegetated versus vegetated areas. Initial analyses indicated that more complex vegetation classifications were unnecessary. Digital soil data were used to stratify major soil orders, while soil drainage indices were used to represent soil moisture conditions. Finally, to characterize stand ages for forested sites, we included age since last fire. Interactions were further explored for vegetation, age, and soil drainage, while non-linear responses were examined for elevation and soil drainage.

TABLE I. GIS predictor variables used for modeling the presence of bear foods in Jasper National Park using logistic regression. Data from the Yellowhead Ecosystem Working Group (YEWG) ecological land classification (Gordon *et al.*, 1998) were used as well as other digital GIS data (*e.g.*, digital elevation model [DEM]).

Variable Code	Name	Response Type	GIS Data Source
hil	hillshade	continuous	DEM spatial analyst hillshade model; 225° aspect and 45° slope = max
elv	elevation	continuous	100-m digital elevation model (DEM)
elv <sup>2</sup>	quadratic of elevation	continuous	100-m digital elevation model (DEM)
veg	vegetation	categorical	reclassification of YEWG vegetation classification (forest versus open)
sdr	soil drainage	continuous	YEWG soil drainage class
sdr <sup>2</sup>	quadratic of sdr	continuous	YEWG soil drainage class
bar	barren areas	categorical	reclassification of barren/unvegetated areas from vegetation classification
bru	brunisol soils	categorical	YEWG reclassification of soil order great group into brunisol/non-brunisol soils
age	successional age	continuous	digital fire history data
veg*age	interaction of veg and age	continuous	reclassified vegetation and fire history layers
veg*sdr	interaction of veg and sdr	continuous	reclassified vegetation and soil drainage layers

A grid size of 100 m was used for all environmental data and resulting food models, as it was the largest grain within our GIS. The 1,343 field vegetation plots were *K*-fold partitioned (randomly divided) into a model training (90%) and model testing (10%) dataset (special case, *K* = 2), allowing for within-sample cross-validation (Fielding & Bell, 1997). Model selection procedures for each species followed a forward minimum-AIC selection method (SWAIC) in STATA, where variables were added, based on AIC scores, until parsimony was achieved (Burnham & Anderson, 1998; Anderson, Burnham & Thompson, 2000). Hosmer and Lemeshow's (1980) goodness-of-fit statistic ( $\hat{C}$ ) and area-under-the-curve estimates from receiver operating characteristic (ROC) curves (Swets, 1988) were used to assess model fit and performance for both model training and model testing (validation) datasets. Model performance was assessed for ROC scores based on three categories. ROC values ranging between 0.5 and 0.7 were taken to represent low model accuracy, while values between 0.7 and 0.9 were considered good model accuracy and those above 0.9 indicated high model accuracy (Swets, 1988; Manel, Williams & Ormerod, 2001).

Following model development, optimal probability cut-off points for prediction of species presence were determined through the optimization of sensitivity and specificity curves from ROC plots (Zweig & Campbell, 1993). Given these cut-off values, maps were generated for each species, where species were either predicted present or absent in each 100-m pixel. Food importance values from Kansas and Riddell (1995) were assigned to individual species, by month per landscape pixel. Importance values for each species and month ranged from seasonally "critical" foods (value of 10) to food items phenologically not available or used (value of 0). For each pixel, food importance values were summed across species for each month (April to October) to obtain final monthly food index values. Final food indices were scaled (based on maximum monthly value) to range between 0 (low importance) and 10 (high importance) to match existing habitat-index models for the park.

#### FOOD-PROBABILITY MODELS

As an alternative to food-index models that assume a particular importance value for each species/month combination and assuming that the appropriate probability cut-off value for prediction was chosen correctly, we maintained the original probability function (0 to 1) for each species. We then used species-specific food probability models in each month as potential predictors of grizzly bear occurrence. Because logistic regression is sensitive to collinearities among explanatory variables (Hosmer & Lemeshow, 1989), we excluded species that were highly correlated ( $r > 0.75$ ) with species already included in models and explaining variation. We verified that final model coefficients were unaffected by collinearity through the examination of variance inflation factors (VIF) using the REGRESS and VIF functions in STATA on a randomly generated dependent variable. Collinearity was assumed to be occurring when individual VIF scores were greater than ten or the mean of all VIFs was considerably larger than one (Chatterjee, Hadi & Price, 2000). Final model selection procedures followed a forward minimum AIC selection.

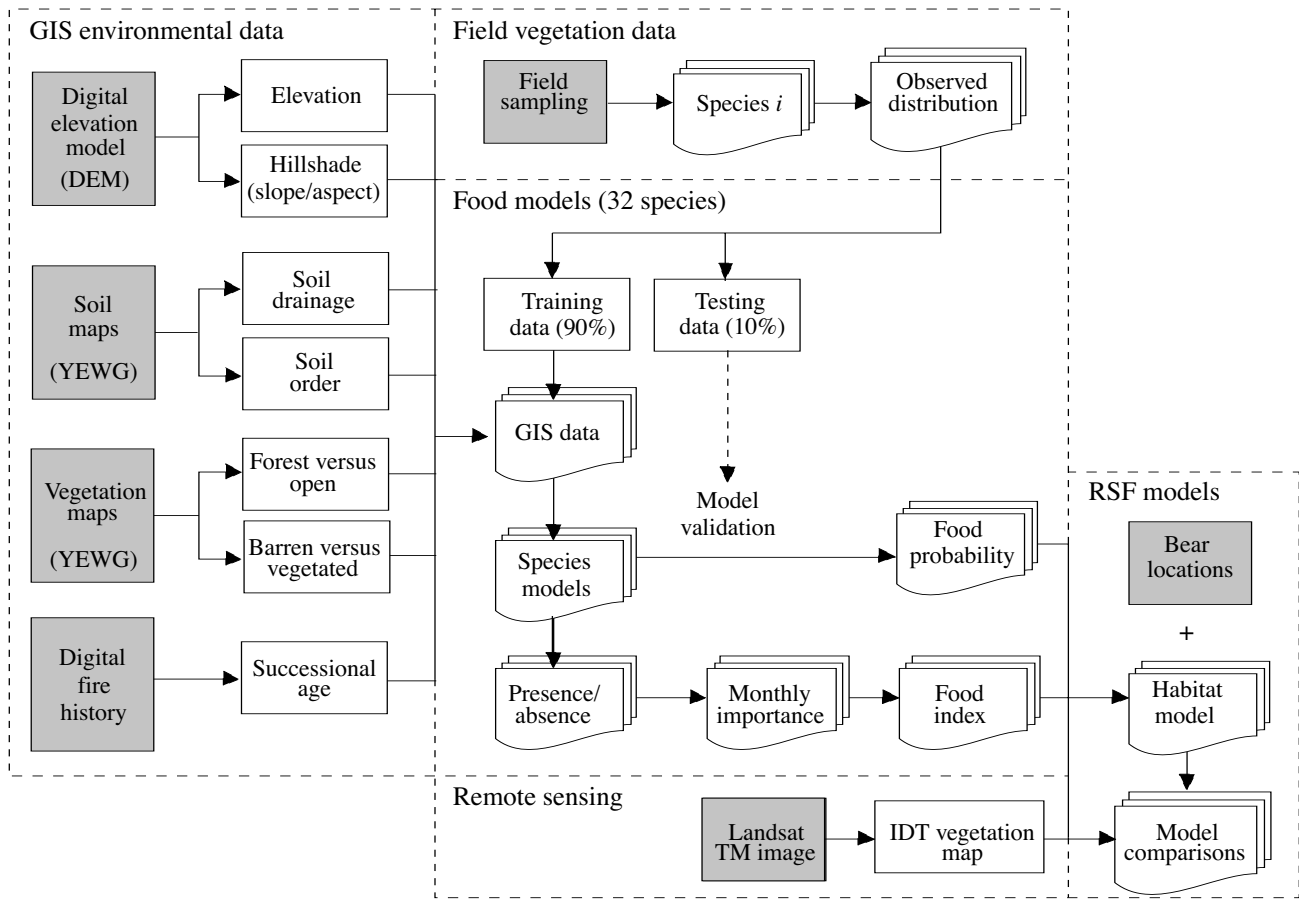


FIGURE 2. Model flow chart depicting covariates from a geographic information system (GIS), food-modeling approaches, and habitat-model resource selection function (RSF) comparisons.

GRIZZLY BEAR RADIOTELEMETRY DATA

In 1999 and 2000, we used aerial darting and leg snaring techniques to capture and collar 10 grizzly bears (8 female and 2 male) in eastern JNP. Bears were fitted with Televilt or ATS (Advanced Telemetry Systems) GPS radiocollars. In total, 3,924 GPS radiolocations from the secondary study area were retrieved between April and October of 1999 and 2000. Locations used for monthly model development varied from 77 locations in April to 936 in June. Because non-random errors from terrain and habitat interference were likely present in missing GPS data (Obbard, Pond & Perera, 1998; Dussault *et al.*, 1999; Rettie & McLoughlin, 1999), interpretation of coefficients should be viewed with caution. Model comparisons from the same dataset, however, are considered robust. Minimum home range convex polygons (100% MCP) were generated for each bear for all data between 1999 and 2000. From these home range polygons, available resources were generated for comparisons with use locations using an equal-area based (1 random point per home range ha) random sampling of GIS environmental data (habitat models).

GRIZZLY BEAR RSF MODELING STRATEGY

We evaluated patch or third-order (Johnson, 1980) resource selection, by month, for grizzly bears in JNP using the above three habitat models (IDT remote-sensing habitat

map, food-index model, and food-probability model). Used resources units from GPS radiotelemetry locations were compared with random samples of available resource units to obtain a resource selection function (RSF) using logistic regression in the program STATA. RSF model structure followed the form

$$w(x) = \exp(\beta_1x_1 + \beta_2x_2 + \dots + \beta_kx_k), \quad [1]$$

where  $w(x)$  is the resource selection function and  $\beta_i$  the selection coefficient estimated for environmental predictors  $x_i$  (Manly, McDonald & Thomas, 1993). For the categorical remote-sensing map, we used the most common habitat cover class, non-vegetated areas, as the reference category. Models were developed at the population level, pooling sexes. We used the robust cluster method to calculate variances around each parameter (Nielsen *et al.*, 2002). Using such a method, we assume the unit of replication to be the individual, not the telemetry location, thus avoiding pseudo-replication/autocorrelation problems (Otis & White, 1999; Nielsen *et al.*, 2002). Three models (remote-sensing map, food probability, and food index) for each month (one for each habitat model) were generated and compared against each other using an AIC information-theoretic model selection design (Anderson, Burnham & Thompson, 2000). Models were AIC ranked ( $\Delta_i$ ) within each month, and the relative likelihood of a model being the best, given the data and models, was estimated using Akaike weights ( $w_i$ ).

**Results**

FOOD-INDEX AND FOOD-PROBABILITY MODELS

Goodness-of-fit tests ( $\hat{C}$ ) for model training data confirmed agreement between the model and data for 25 of 32 species, while ROC values  $> 0.7$  (representing good model performance) occurred in 28 of 32 species (Table II). Six of these 28 ROC values were  $> 0.9$ , indicating high model accuracy. Validation of training models using withheld testing data dropped the total number of fit species to 22, while validated ROC estimates pointed to reasonable classification accuracy for 25 of the 32 species. Five of these species had high model accuracy. Common predictor variables chosen for final AIC-selected models included elevation (linear and non-linear responses), hillshade, age of stand, soil drainage (linear and non-linear responses), and the interaction of vegetation and age (Table II). Using estimated coefficients from each model, the probability of occurrence for each food species was estimated across JNP using a GIS. An example of a probability model, estimated for *Shepherdia canadensis*, is illustrated in figure 3. Resulting probability maps, by species, were subsequently used for estimating monthly grizzly bear occurrence (food-probability RSF models).

Using these same food models, optimal probability cut-off values for each species were estimated from sensitivity and specificity graphs from ROC calculations. Optimal cut-

off values ranged from 1.76% for *Rubus idaeus* to 35.77% for *Juniperus* spp. (Table II). Based on these cut-off values, the presence/absence of each species was estimated across JNP using a reclassification of the original probability levels in a GIS. Qualitative food values were assigned for each species in each month (Kansas & Riddell, 1995) for predicted (presence) grid cells resulting in monthly food-index maps that were used for estimating grizzly bear occurrence (food-index RSF models). Examination of monthly food-index models revealed that the largest proportion of high-quality habitats existed in the Athabasca River valley where the greatest diversity of foods exists.

GRIZZLY BEAR RSF HABITAT MODEL COMPARISONS

Model assessments using AIC weights ( $w_i$ ) indicated that food-index models developed for all seven months inadequately described grizzly bear occurrence in JNP (all months;  $w_i < 0.001$ ). By comparison, the food-probability models and the remote-sensing model both performed substantially better than food-index models (Table III). In April and July, the remote-sensing model had the greatest model support within the candidate sets, at likelihoods of 80.4% and 98.7% respectively. The predicted relative probability of occurrence for grizzly bears in July, using the AIC-selected remote-sensing model, is illustrated in figure 4.

TABLE II. Comparison of model performance and fit for AIC-selected logistic regression models for 32 species of plants known to be important grizzly bear foods in Jasper National Park. Model training data (90%), as well as model-testing data (10%), were used for assessing models. Hosmer-Lemeshow goodness-of-fit criterion ( $\hat{C}$ )  $p$ -values are reported ( $p\hat{C}$ ), as well as area-under-curve estimates from receiver operator characteristics (ROC). ROC values ranging from 0.7 to 0.9 were considered to have reasonably good model performance, while ROC values exceeding 0.9 were considered to be highly accurate. Optimal probability cut-off point is the location where species were predicted present or absent in GIS food-index models.

Species	AIC Model	Optimal	Model Training		Model Testing	
		Cut-off	$p\hat{C}$	ROC	$p\hat{C}$	ROC
<i>Achillea millefolium</i>	hil+veg+age+veg*age	0.1399	0.654	0.674	0.750	0.713
<i>Amelanchier alnifolia</i>	hil+elv <sup>2</sup>	0.0521	0.000	0.923	0.999	0.949
<i>Arctostaphylos uva-ursi</i>	hil+elv+age+sdr	0.2072	0.926	0.814	0.018	0.734
<i>Aster</i> spp.	hil+age+elv <sup>2</sup>	0.2326	0.607	0.876	0.000	0.772
<i>Astragalus</i> spp.	sdr <sup>2</sup>	0.0689	0.649	0.668	0.088	0.520
<i>Claytonia lanceolata</i>	veg+elv+elv <sup>2</sup> +sdr <sup>2</sup>	0.0391	0.968	0.860	0.312	0.975
<i>Cornus stolonifera</i>	elv	0.0216	0.968	0.972	1.000	0.984
<i>Empetrum nigrum</i>	hil+elv+elv <sup>2</sup> +sdr+bar+bru	0.1863	0.594	0.744	0.000	0.815
<i>Equisetum arvense</i>	hil+elv <sup>2</sup> +sdr+veg*age	0.0787	0.774	0.703	0.880	0.762
<i>Fragaria virginiana</i>	hil+veg+elv <sup>2</sup> +age+veg*age	0.2599	0.879	0.722	0.294	0.727
<i>Hedysarum</i> spp.	hil+veg+sdr <sup>2</sup> +bar+bru+veg*sdr	0.1323	0.894	0.821	0.379	0.704
<i>Heracleum lanatum</i>	hil+elv+elv <sup>2</sup> +age+veg*age	0.0290	0.112	0.795	0.042	0.793
<i>Juniperus</i> spp.	hil+veg+elv+elv <sup>2</sup> +age+sdr+bar+bru+for*age+veg*sdr	0.3577	0.688	0.753	0.390	0.719
<i>Lathyrus ochroleucus</i>	hil+elv+elv <sup>2</sup> +age+sdr <sup>2</sup> +bru+veg*age	0.0493	0.995	0.932	0.221	0.890
<i>Lonicera</i> spp.	elv+elv <sup>2</sup> +age	0.0757	0.099	0.891	0.893	0.910
<i>Ribes</i> spp.	hil+elv+elv <sup>2</sup> +bru	0.1161	0.921	0.791	0.409	0.890
<i>Rosa acicularis</i>	hil+elv <sup>2</sup> +age+sdr+sdr <sup>2</sup>	0.2744	0.358	0.912	0.455	0.893
<i>Rubus idaeus</i>	elv+elv <sup>2</sup> +age+veg*age	0.0176	0.251	0.833	0.868	0.922
<i>Rubus</i> spp.	hil+elv+elv <sup>2</sup> +age+sdr+sdr <sup>2</sup> +bru	0.1040	0.019	0.711	0.691	0.700
<i>Senecio triangularis</i>	hil+elv+elv <sup>2</sup> +age+sdr <sup>2</sup> +veg*age+veg*sdr	0.1351	0.040	0.811	0.825	0.727
<i>Shepherdia canadensis</i>	hil+elv+elv <sup>2</sup> +age+sdr+sdr <sup>2</sup>	0.3860	0.327	0.866	0.483	0.847
<i>Sorbus</i> spp.	hil+veg+elv+elv <sup>2</sup> +sdr+sdr <sup>2</sup> +veg*sdr	0.0339	0.304	0.820	0.966	0.890
<i>Thalictrum</i> spp.	age+bar	0.0716	0.274	0.713	0.637	0.694
<i>Vaccinium caespitosum</i>	veg*sdr	0.1798	0.023	0.674	0.172	0.667
<i>Vaccinium membranaceum</i>	hil+bru+veg*age	0.2588	0.097	0.757	0.000	0.733
<i>Vaccinium myrtillus</i>	veg*sdr	0.0271	0.326	0.695	0.000	0.678
<i>Vaccinium scoparium</i>	elv+elv <sup>2</sup> +age+bru+veg*sdr	0.2453	0.011	0.733	0.000	0.695
<i>Vaccinium vitis-idaea</i>	hil+veg+elv+elv <sup>2</sup> +age+sdr+veg*age	0.2375	0.105	0.732	0.020	0.785
<i>Valeriana sitchensis</i>	hil+veg+elv+elv <sup>2</sup> +age+bar+bru+veg*age	0.1403	0.000	0.806	0.495	0.696
<i>Veratrum eschscholtzii</i>	hil+elv+elv <sup>2</sup> +age+sdr <sup>2</sup> +bar+veg*age+veg*sdr	0.0538	0.781	0.826	0.000	0.646
<i>Viburnum edule</i>	elv+elv <sup>2</sup>	0.1139	0.000	0.902	0.923	0.903
<i>Vicia americana</i>	hil+elv+elv <sup>2</sup>	0.0689	0.399	0.929	0.000	0.755

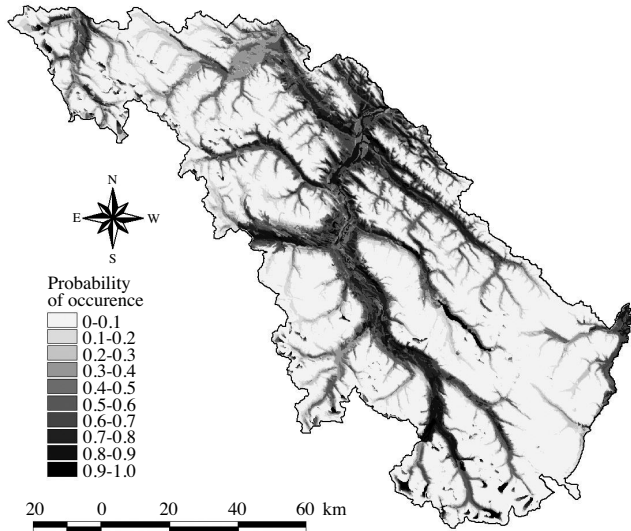


FIGURE 3. Probability of occurrence for *Shepherdia canadensis* in Jasper National Park based on variables hillshade, elevation (non-linear), stand age, and soil drainage (non-linear).

TABLE III. A comparison of habitat GIS models used for predicting the relative occurrence of grizzly bears (resource selection functions) in Jasper National Park (JNP), Alberta. Models were assessed through the ranking of AIC values ( $\Delta_i$ ) and weights ( $w_i$ ) describing the likelihood of the model. Model complexity (number of parameters) is represented by  $K_i$ . Models were compared among months (April to October). The IDT (Integrated Decision Tree) model represented a Landsat-TM-based habitat cover map. Food-probability models (by month) were derived from AIC-selected (minimum AIC, forward selection) predictive food models from the 32 available resources (plant species). Food-index models represent qualitative indices (0-10) of food values for predicted food items (from probability models) by month following Kansas and Riddell (1995).

Month	Model	$K_i$	AIC	$\Delta_i$	$w_i$
April	IDT Model	4	504.08	0	0.804
	Food-Probability Model	4	506.91	2.83	0.195
	Food-Index Model	2	519.25	15.17	<0.001
May	Food-Probability Model	10	3,404.82	0	1.000
	IDT Model	5	3,668.58	263.76	<0.001
	Food-Index Model	2	3,784.44	379.62	<0.001
June	Food-Probability Model	5	3,838.76	0	1.000
	IDT Model	5	3,867.08	28.32	<0.001
	Food-Index Model	2	4,106.2	267.44	<0.001
July	IDT Model	5	3,210.56	0	0.987
	Food-Probability Model	13	3,219.27	8.71	0.013
	Food-Index Model	2	3,700.02	489.46	<0.001
August	Food-Probability Model	12	3,192.04	0	1.000
	IDT Model	5	3,225.08	33.04	<0.001
	Food-Index Model	2	3,664.3	472.26	<0.001
September	Food-Probability Model	10	1,529.12	0	1.000
	IDT Model	5	1,673.24	144.12	<0.001
	Food-Index Model	2	1,753.54	224.42	<0.001
October	Food-Probability Model	8	1,435.6	0	1.000
	IDT Model	5	1,570.94	135.34	<0.001
	Food-Index Model	2	1,772.56	336.96	<0.001

Selection of classified remote-sensing habitat classes varied substantially among months. For instance, bears were 14 times more likely (odds ratio) to use alpine habitats in July than in May, while a substantial increase in selection of shrub/wetland habitats was evident in September (Figure 5).

In five of seven months (May, June, August, September, and October), food-probability models out performed remote-sensing models. The relative likelihood of support for these models was 100%, given the data and models tested. Spatial predictions of the relative probability of occurrence for grizzly bears in May and August using food-probability models are illustrated in figure 4. As would be expected, there were strong patterns of selection relating to the terrain features, as large areas of rock and ice exist throughout the park. The number of species, composition of species, and the direction and magnitude of responses varied among months (Table IV). The simplest model (June) contained the species *Achillea millefolium*, *Claytonia lanceolata*, *Heracleum lanatum*, and *Thalictrum* spp., while the most complex model (August) included *Astragalus* spp., *Claytonia lanceolata*, *Cornus stolonifera*, *Fragaria virginiana*, *Hedysarum* spp., *Heracleum lanatum*, *Rubus idaeus*, *Vaccinium scoparium*, *V. vitis-idaea*, *Valeriana sitchensis*, and *Verartrum eschscholtzii*. Foods that consistently contributed to monthly grizzly bear RSF models included *Claytonia lanceolata*, *Astragalus* spp., *Hedysarum* spp., *Rubus idaeus*, and *Thalictrum* spp. (Table IV). A number of food-probability RSF models contained species with negative coefficients, indicating apparent avoidance or under-sampling of areas associated with those foods. Other species that were expected to show strong seasonal selection due to locally recognized “critical” importance, such as *Shepherdia canadensis*, failed to exhibit strong patterns of selection.

### Discussion

Grizzly bear food resources in Jasper National Park were principally related to elevation, hillshade, age of stand, soil drainage, and the interaction of vegetation and age. Non-linear responses were common for the variables elevation and soil drainage, with species optimizing at intermediate levels. Food-index maps produced from the predicted presence of each species and monthly food values (Kansas & Riddell, 1995) proved poor predictors of grizzly bear occurrence. Food-probability models based on the same data and models, however, were good predictors of grizzly bear occurrence. The disconnect between food-index and food-probability models may relate to inappropriate classification thresholds (ROC) used for predicting species presence (Manel, Williams & Ormerod, 2001) or to problems inherent in food importance values developed by Kansas and Riddell (1995). The use of habitat-effectiveness models in the four contiguous parks of Canada (Gibeau, 1998; Hood & Parker, 2001) should consider further validation of food-importance values or alternative modeling approaches (e.g., RSF-based). We found for instance, substantial improvement over food-index models in the prediction of grizzly bear occurrence using a simple remote-sensing classification (Franklin *et al.*, 2001).

Food-probability models demonstrated consistent successful prediction of grizzly bear occurrence, with model evidence highest in five of seven months (May, June, August, September, and October). Coefficients from these models may be useful surrogates of food-importance values. The remote-sensing habitat model was favoured in April and July. We are uncertain why the July remote-sensing

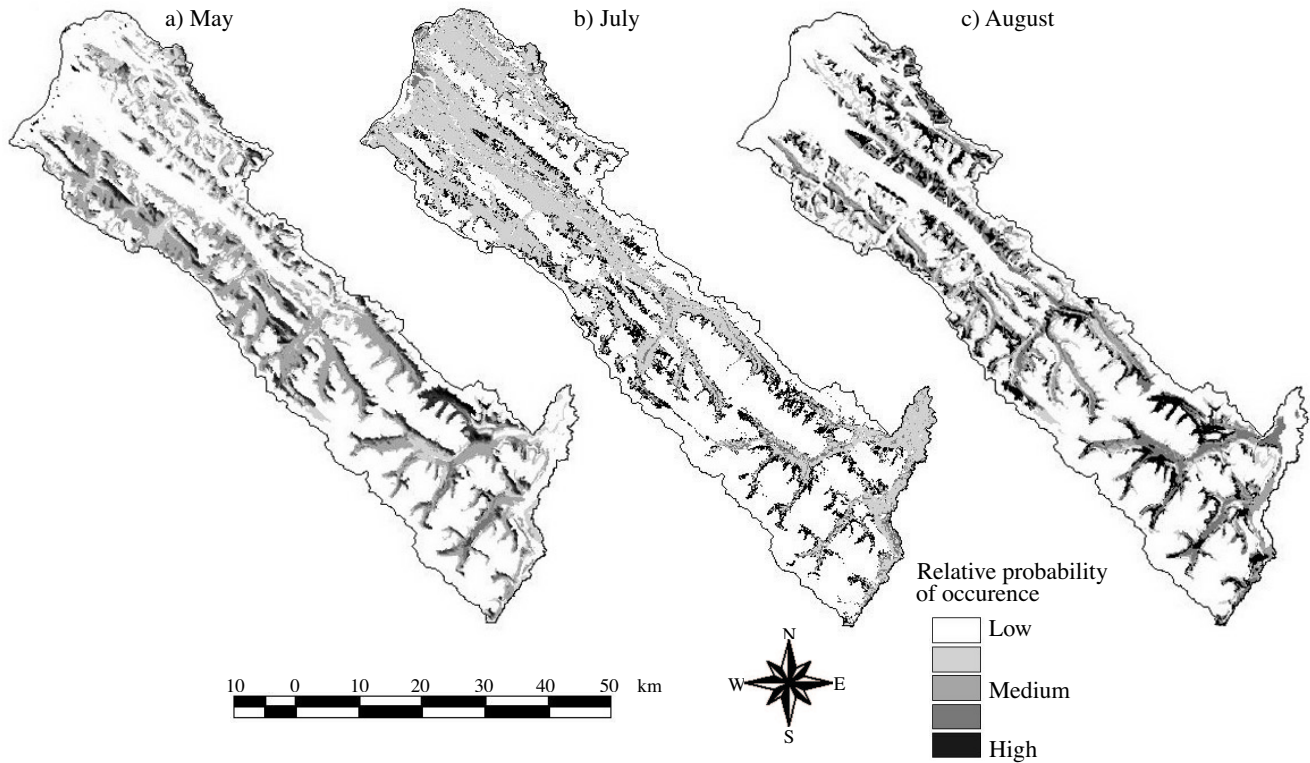


FIGURE 4. Example of final AIC-selected resource selection function (RSF) models for the secondary study area in eastern Jasper National Park, Alberta. The three months depicted are a) May, b) July, and c) August. July predictions are based on a remote-sensing vegetation map, while both May (a) and August (c) illustrate predictions based on food-probability models.

TABLE IV. Estimated model parameters for AIC-selected grizzly bear food-probability resource selection function (RSF) models describing grizzly bear occurrence for Jasper National Park. Coefficients and standard errors (in parentheses) are presented by species.

Species	Month						
	April	May	June	July	August	September	October
<i>Achillea millefolium</i>	12.11 (1.50)	3.49 (0.89)	6.53 (2.93)				
<i>Amelanchier alnifolia</i>							
<i>Arctostaphylos uva-ursi</i>		-3.45 (1.18)		-9.98 (1.76)			
<i>Aster</i> spp.							
<i>Astragalus</i> spp.				21.79 (10.78)	16.26 (4.91)	24.82 (23.97)	
<i>Claytonia lanceolata</i>	11.72 (9.61)	19.41 (2.00)	8.07 (1.54)	20.41 (5.72)	16.95 (2.42)	24.02 (5.45)	26.41 (2.84)
<i>Cornus stolonifera</i>				-1,749.97 (1,199.85)	-2,999.03 (523.52)	-1,089.26 (221.90)	-2,349.92 (2,285.87)
<i>Empetrum nigrum</i>							-4.29 (4.27)
<i>Equisetum arvense</i>	10.37 (6.35)	9.73 (2.05)					
<i>Fragaria virginiana</i>					-2.99 (1.05)		
<i>Hedysarum</i> spp.		2.30 (0.76)		2.80 (1.18)	2.03 (1.01)	3.84 (2.66)	
<i>Heracleum lanatum</i>			-9.62 (2.98)	-23.14 (10.47)	-59.80 (8.88)		
<i>Juniperus</i> spp.	2.42 (0.49)					-4.01 (2.22)	2.06 (0.61)
<i>Lathyrus ochroleucus</i>		-11.51 (4.93)		39.81 (15.53)			
<i>Lonicera</i> spp.							
<i>Ribes</i> spp.							9.13 (10.84)
<i>Rosa acicularis</i>							
<i>Rubus idaeus</i>				184.83 (88.53)	272.84 (42.63)		
<i>Rubus</i> spp.						5.19 (4.84)	
<i>Senecio triangularis</i>		-2.38 (1.31)					
<i>Shepherdia canadensis</i>						5.795 (1.340)	
<i>Sorbus</i> spp.							
<i>Thalictrum</i> spp.		9.85 (3.40)	23.25 (2.00)				
<i>Vaccinium cespitosum</i>						30.25 (11.01)	
<i>Vaccinium membranaceum</i>							
<i>Vaccinium myrtillus</i>							96.98 (30.58)
<i>Vaccinium scoparium</i>				9.09 (1.80)	5.77 (0.62)		
<i>Vaccinium vitis-idaea</i>				2.09 (1.88)	8.08 (1.05)		
<i>Valeriana sitchensis</i>					12.14 (1.12)		
<i>Veratrum eschscholtzii</i>		3.69 (1.15)		2.91 (3.61)	-3.44 (1.97)	-6.71 (6.14)	-18.34 (12.11)
<i>Viburnum edule</i>							
<i>Vicia americana</i>							

model was more useful, when the importance of plant foods during this period should be substantial. Berries begin to become available during this time and succulent vegetation is near its optimum. Lack of support for July food models was also consistent with model assessments made by Kansas and Riddell (1995). In an examination of remotely sensed habitat classes and bear locations, it was apparent that selection during July was most evident for alpine habitats (Figure 5). Because plant foods are scarce in April, it was less surprising to find lack of support for food models during this period.

Due to limitations in GIS data, we were forced to impose a spatial grain (minimum mapping unit) of 100 m for food models. Although this appeared to work reasonably well for simple presence/absence data, more complex food measures, such as food productivity, density, or cover, may be too variable to be modeled at such a large spatial grain. Food microsites, such as patches of *Equisetum arvense* in small wet seeps, were not likely represented well at this scale and with currently used GIS and remote-sensing data. Habitat quality surrogates, such as a tasseled cap greenness transformation from remote-sensing data, may be useful for mapping such microsites if used with high-resolution multi-spectral sensors such as IKONOS or ASTER.

Fundamental food resources used by grizzly bears appear to be phenologically driven at temporal scales rarely addressed in previous habitat selection studies (see, however, Mattson, 2000). We found selection of resources and habitats to be highly variable temporally. Analyzing selection of habitats and/or resources for longer periods (*i.e.*, 2- or 4-season models) likely will mask important selection processes operating at finer scales (Schooley, 1994). Avoidance of some food items thought to be important *a priori*, such as *Cornus stolonifera*, was apparent in model estimates. Such foods tended to correlate with low elevation sites in the Athabasca River valley, where sample grizzly bear locations were largely absent and thus may have influenced final model estimates. Interpretation of coefficients for species like *Cornus stolonifera*, having large negative values, should therefore be viewed with caution. However,

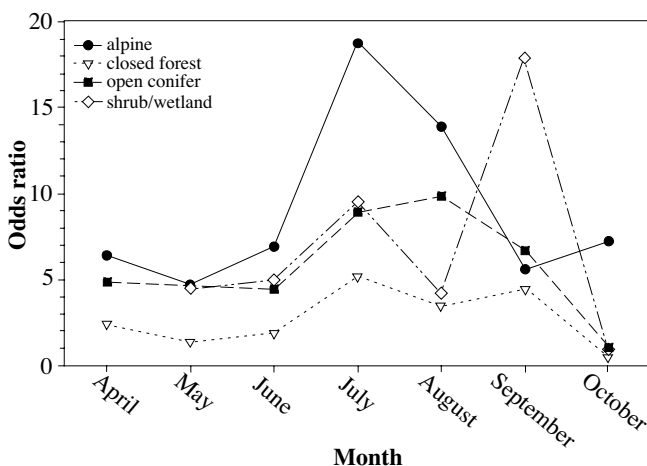


FIGURE 5. Seasonal variation in habitat selection of grizzly bears for four habitat cover classes in Jasper National Park, Alberta. All reported odds ratios are in comparison (reference category) to the most abundant habitat class, non-vegetated areas.

most grizzly bear plant foods used for food-probability RSF models correspond well with feeding observations and feces examinations for regional grizzly bear populations (Holcroft & Herrero, 1984; Hamer & Herrero, 1987; Hamer, Herrero & Brady, 1991; Hamer, 1996). Incorporation of non-plant foods, especially ants, carrion, and ungulate calves, should be further explored to increase food model accuracy and realism. This seems particularly relevant for male grizzly bears, because their diets tend to contain larger contributions of meat (Jacoby *et al.*, 1999). We pooled all animals (sexes, ages, etc.) in these analyses, which may have affected parameter estimates and variances. Strong variation in habitat selection among individuals has been described in this population (Nielsen *et al.*, 2002). Further caution should be given to the interpretation and use of coefficients because they may be affected by GPS fix acquisition bias associated with terrain and habitat structure (Dussault *et al.*, 1999) and because covariates obtained from GIS contained unknown measurement errors.

Indirect GIS and remotely sensed data have been relied upon for prediction of landscape-scale grizzly bear habitats (Mace *et al.*, 1996; Mace *et al.*, 1999; Boyce & Waller, 2000; Nielsen *et al.*, 2002). The tasseled cap greenness transformation (Crist & Cicone, 1984; Manley, Ake & Mace, 1992) has been shown, for example, to be a strong predictor of grizzly bear occurrence. However, there is little information on what greenness actually represents beyond high vegetative reflectance and leaf-area index (White *et al.*, 1997; Waring & Running, 1998). Mechanistic links are needed to describe whether relationships exist with grizzly bear foods and/or fitness. Understanding such relationships will better facilitate use of habitat models for conservation and management planning. We believe that incorporation of direct food models, especially under phenological scales, is an important development for grizzly bear habitat modeling. Such direct resource gradients more closely correspond to the resources perceived and used by the animal.

### Acknowledgements

Data presented in this paper represent one component of the Foothills Model Forest Grizzly Bear Research Program. Funding was provided by Ainsworth Lumber, Alberta Conservation Association (ACA), ACA Biodiversity Grants, 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, Canadian Resources Ltd., Canadian Forest Products, Canadian Hunter, Canadian Wildlife Service, Cardinal River Coals Ltd., Foothills Model Forest, FS Chia PhD Scholarship, 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, PTAC (Petroleum Technology Alliance of Canada), Rocky Mountain Elk Foundation, Suncor, Sundance Forest Industries, Sunpine Forest Products Ltd., Telemetry Solutions, The Centre for Wildlife Conservation (U.S.A.), Trans Canada Pipeline, University of Alberta, University of Calgary, University of Lethbridge, University of Washington, Weldwood of Canada Ltd., Western College of Veterinary Medicine, Weyerhaeuser Canada Ltd., and World Wildlife Fund. M. Cattet, N. Caulkett, B. Goski, J.



Lee, M. Urquhart, and a number of Alberta Conservation Officers provided expertise and support during bear capture. C. Popplewell and J. Dugas provided GIS support. H. Purves (Parks Canada) and P. Achuff (Parks Canada) provided field vegetation data from Jasper National Park. We thank C. Johnson, N. C. Stenseth (Associate Editor) and two anonymous referees for reviewing the manuscript and providing generous comments.

### Literature cited

- Anderson, D. R., K. P. Burnham & W. L. Thompson, 2000. Null hypothesis testing: Problems, prevalence, and an alternative. *Journal of Wildlife Management*, 64: 912-923.
- Anonymous, 1998. Cumulative Effects Assessment (CEA) Application for Grizzly Bears. Version 1. Users Guide. Jasper National Park, Jasper, Alberta.
- Boyce, M. S. & L. L. McDonald, 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution*, 14: 268-272.
- Boyce, M. S. & J. S. Waller, 2000. The application of resource selection functions analysis to estimate the number of grizzly bears that could be supported by habitats in the Bitterroot ecosystem. Pages 6-231 to 6-241 in C. Servheen (ed.). *Grizzly Bear Recovery in the Bitterroot Ecosystem. Final Environmental Impact Statement. Appendix 21B*. U.S. Fish & Wildlife Service, Missoula, Montana.
- Burnham, K. P. & D. R. Anderson, 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Chatterjee, S., A. S. Hadi & B. Price, 2000. *Regression Analysis by Example*. 3<sup>rd</sup> edition. John Wiley & Sons, New York.
- Clark, T. W., P. C. Paquet & A. P. Curlee, 1996. Introduction to special section: Large carnivore conservation in the Rocky Mountains of the United States and Canada. *Conservation Biology*, 10: 936-939.
- Crist, E. P. & R. C. Cicone, 1984. Application of the tasseled cap concept to simulated thematic mapper data. *Photogrammetric Engineering and Remote Sensing*, 50: 343-352.
- Dussault, C., R. Courtois, J. P. Ouellet & J. Huot, 1999. Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. *Wildlife Society Bulletin*, 27: 965-972.
- Fielding, A. H. & J. F. Bell, 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24: 38-49.
- Franklin, S. E., G. B. Stenhouse, M. J. Hansen, C. C. Popplewell, J. A. Dechka & D. R. Peddle, 2001. An integrated decision tree approach (IDTA) to mapping landcover using satellite remote sensing in support of grizzly bear habitat analysis in the Alberta Yellowhead Ecosystem. *Canadian Journal of Remote Sensing*, 27: 579-592.
- Garshelis, D. L., 2000. Delusions in habitat evaluation: Measuring use, selection, and importance. Pages 111-164 in L. Boitani & T. K. Fuller (ed.), *Research Techniques in Animal Ecology: Controversies and Consequences*. Columbia University Press, New York.
- Gibeau, M. L., 1998. Grizzly bear habitat effectiveness model for Banff, Yoho, and Kootenay National Parks, Canada. *Ursus*, 10: 235-241.
- Gordon, S., J. Bentz, D. O'Leary & D. Clish, 1998. *Common Ecological Land Classification and Associated Attribute Database for the Yellowhead Ecosystem*. 2<sup>nd</sup> edition. GEOWEST Environmental Consultants Ltd., Edmonton, Alberta.
- Hamer, D., 1996. Buffaloberry [*Shepherdia canadensis* (L.) Nutt.] fruit production in fire-successional bear feeding sites. *Journal of Range Management*, 49: 520-529.
- Hamer, D. & S. Herrero, 1987. Grizzly bear food and habitat in the Front Ranges of Banff National Park, Alberta. *International Conference on Bear Research and Management*, 7: 199-213.
- Hamer, D., S. Herrero & K. Brady, 1991. Food and habitat used by grizzly bears, *Ursus arctos*, along the Continental Divide in Waterton Lakes National Park, Alberta. *Canadian-Field Naturalist*, 105: 325-329.
- Holcroft, A. C. & S. Herrero, 1984. Grizzly bear digging sites for *Hedysarum sulphurescens* roots in southwestern Alberta. *Canadian Journal of Zoology*, 62: 2571-2575.
- Holland, W. D. & G. M. Coen, 1982. *Ecological (Biophysical) Land Classification of Banff and Jasper National Parks. Volume II. Soil and Vegetation Resources*. Alberta Institute of Pedology Publication No. SS-82-44, Edmonton, Alberta.
- Honacki, J. H., K. E. Kinman & J. W. Koepl, 1982. *Mammal Species of the World: A Taxonomic and Geographic Reference*. Allen Press and The Association of Systematics Collections, Lawrence, Kansas.
- Hood, G. A. & K. L. Parker, 2001. Impact of human activities on grizzly bear habitat in Jasper National Park. *Wildlife Society Bulletin*, 29: 624-638.
- Hosmer, D. W., Jr. & S. Lemeshow, 1980. Goodness-of-fit tests for the multiple logistic regression model. *Communications in Statistics*, A9: 1043-1069.
- Hosmer, D. W., Jr. & S. Lemeshow, 1989. *Applied Logistic Regression*. John Wiley & Sons, New York.
- Jacoby, M. E., G. V. Hilderbrand, C. Servheen, C. C. Schwartz, S. M. Arthur, T. A. Hanley, C. T. Robbins & R. Michener, 1999. Trophic relations of brown and black bears in several western North American ecosystems. *Journal of Wildlife Management*, 63: 921-929.
- Johnson, D. H., 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61: 65-71.
- Kansas, J. L. & R. N. Riddell, 1995. *Grizzly Bear Habitat Model for the Four Contiguous Mountain Parks. Second Iteration*. Riddell Environmental Research Ltd., Red Deer, Alberta and URSUS Ecosystem Management Ltd., Calgary, Alberta.
- La Roi, G. H. & R. J. Hnatiuk, 1980. The *Pinus contorta* forests of Banff and Jasper National Parks: A study in comparative synecology and syntaxonomy. *Ecological Monographs*, 50: 1-29.
- Lennon, J. J., 1999. Resource selection functions: Taking space seriously. *Trends in Ecology and Evolution*, 14: 399-400.
- Mace, R. D., J. S. Waller, T. L. Manley, L. J. Lyon & H. Zuuring, 1996. Relationship among grizzly bears, roads and habitat in the Swan Mountains, Montana. *Journal of Applied Ecology*, 33: 1395-1404.
- Mace, R. D., J. S. Waller, T. L. Manley, K. Ake & W. T. Wittinger, 1999. Landscape evaluation of grizzly bear habitat in western Montana. *Conservation Biology*, 13: 367-377.
- Manel, S., H. C. Williams & S. J. Ormerod, 2001. Evaluating presence-absence models in ecology: The need to account for prevalence. *Journal of Applied Ecology*, 38: 921-931.
- Manley, T. L., K. Ake & R. D. Mace, 1992. Mapping grizzly bear habitat using Landsat TM satellite imagery. Pages 231-240 in J. D. Greer (ed.). *Remote Sensing and Natural Resource Management*. American Society of Photogrammetry and Remote Sensing, Bethesda, Maryland.
- Manly, B. F. J., L. L. McDonald & D. L. Thomas, 1993. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Chapman & Hall, London.
- Mattson, D. J., 2000. Causes and consequences of dietary differences among Yellowstone grizzly bears (*Ursus arctos*). Ph.D. thesis, University of Idaho, Moscow, Idaho.

- Mattson, D. J., K. Barber, R. Maw & R. Renkin, 1999. Coefficients of productivity for Yellowstone's grizzly bear habitat. U.S.G.S. Forest and Rangeland Ecosystem Science Center, Moscow, Idaho.
- McLellan, B. N. & V. Banci, 1999. Status and management of the brown bear in Canada. Pages 46-50 in C. Servheen, S. Herrero & B. Peyton (ed.). Bears: Status Survey and Conservation Action Plan. International Union for Conservation of Nature and Natural Resources (IUCN), Gland.
- Mladenoff, D. J., T. A. Sickley, R. G. Haight & A. P. Wydeven, 1995. A regional landscape analysis and prediction of favourable gray wolf habitat in the northern Great Lakes region. *Conservation Biology*, 9: 279-294.
- Morrison, M. L., 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *Journal of Wildlife Management*, 65: 613-623.
- Moss, E. H., 1994. *The Flora of Alberta*. 2<sup>nd</sup> edition. University of Toronto Press, Toronto, Ontario.
- Nielsen, S. E. & A. Haney, 1998. Gradient responses for understory species in a bracken-grassland and northern-dry forest ecosystem of northeast Wisconsin. *Transactions of the Wisconsin Academy of Arts, Letters, and Sciences*, 86: 149-166.
- Nielsen, S. E., M. S. Boyce, G. B. Stenhouse & R. H. M. Munro, 2002. Modeling grizzly bear habitats in the Yellowhead Ecosystem of Alberta: Taking autocorrelation seriously. *Ursus*, 13: 533-542.
- Obbard, M. E., B. A. Pond & A. Perera, 1998. Preliminary evaluation of GPS collars for analysis of habitat use and activity patterns of black bears. *Ursus*, 10: 209-217.
- Otis, D. L. & G. C. White, 1999. Autocorrelation of location estimates and the analysis of radiotracking data. *Journal of Wildlife Management*, 63: 1039-1044.
- Rettie, W. J. & P. D. McLoughlin, 1999. Overcoming radiotelemetry bias in habitat-selection studies. *Canadian Journal of Zoology*, 77: 1175-1184.
- Schooley, R. L., 1994. Annual variation in habitat selection: Patterns concealed by pooled data. *Journal of Wildlife Management*, 58: 367-374.
- Swets, J. A., 1988. Measuring the accuracy of diagnostic systems. *Science*, 240: 1285-1293.
- Waring, R. H. & S. W. Running, 1998. *Forest Ecosystems: Analysis at Multiple Scales*. 2<sup>nd</sup> edition. Academic Press, San Diego, California.
- White, J. D., S. W. Running, R. Nemani, R. E. Keane & K. C. Ryan, 1997. Measurement and remote sensing of LAI in Rocky Mountain montane ecosystems. *Canadian Journal of Forest Research*, 27: 1714-1727.
- Zweig, M. H. & G. Campbell, 1993. Receiver-operating characteristic (ROC) plots: A fundamental tool in clinical medicine. *Clinical Chemistry*, 39: 561-577.