



Dynamic wildlife habitat models: Seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears

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ABSTRACT

Most current wildlife habitat models, such as resource selection functions, typically assume a static environment, extrapolate poorly in space and time, and often lack linkages to population processes. We submit that more mechanistic habitat models that directly consider bottom-up resources affecting growth and reproduction (i.e., food) and top-down limitations affecting survival are needed to effectively predict habitat quality, especially in the presence of rapid environmental change. Here we present a general model for estimating potential habitat quality (relating to growth and reproduction) and realised habitat quality (accounting for survival) using basic knowledge of the species' seasonal diet, predicted locations of food resource patches and regional patterns in mortality risk. We illustrate our model for a threatened population of grizzly bears in west-central Alberta. Bi-monthly potential habitat quality successfully predicted habitat selection by radio-collared grizzly bears, while multi-seasonal realised habitat quality predicted patterns in occupancy-abundance as measured from unique bears at hair-snag sites. Bottom-up resources therefore predicted patterns of habitat selection, while top-down processes (survival) were necessary to scale-up to population measures. We suggest that more direct measures of resources and environments that affect growth, reproduction and survival, as well as match the temporal scale of animal behaviour, be considered when developing wildlife habitat models.

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1. Introduction

In order to anticipate and manage the consequences of landscape change to species habitat, knowledge of habitat requirements are needed. Today most wildlife habitat models are based on patterns of animal use, occupancy or selection using radiotelemetry or field survey data (Johnson et al., 2006). One of the most common approaches, called resource selection functions (RSFs, Manly et al., 2002), is to estimate habitat selection by comparing environmental characteristics at animal use locations with a set of available (random) locations. Habitat selection and occupancy-based estimates, however, may not relate to population measures such as density, questioning their utility for management of populations (Nielsen et al., 2005; Johnson and Seip, 2008). Although environmental covariates describing habitat selection should relate directly to those factors influencing survival (perceived risk

and reproduction or growth (food resource abundance) to ensure relations to population processes, most models are based on readily available surrogates of habitat such as Normalized Difference Vegetation Index (Wiegand et al., 2008) or cover types (Schlossberg and King, 2009). Such models assume that the general distribution of animals (as opposed to population abundance or performance) is sufficient to define habitat quality and that surrogates used to describe habitat adequately relate to food resource abundance. The use of habitat surrogates and habitat selection measures, however, diminish our understanding of critical regulating factors of populations restricting our ability to target management actions. When in the presence of maladaptive habitat selection, the management for selected habitats may even hasten population decline by adding ecological traps/attractive sinks (Schlaepfer et al., 2002; Nielsen et al., 2006, 2008). Knowledge of both top-down limitations to populations (survival) and bottom-up regulation of populations (foods) are therefore needed to properly quantify habitat quality.

Food resources (nutrients/energy) are often a critical regulating factor affecting individual growth of animals and abundance of populations (Miyashita, 1992; Carbone and Gittleman, 2002; Mattson et al., 2004; Brasher et al., 2007). This is particularly true

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for bears because of their high nutritional demands that peak over a short period of time in the summer and fall (hyperphagia) when individuals are accumulating fat to survive winter (Rode et al., 2006; Berland et al., 2008) and during spring for females with growing young (Farley and Robbins, 1995; Rode et al., 2001). Bears attempt to balance intake of foods high in protein with foods high in energy (Rode and Robbins, 2000; Rode et al., 2001; Felicetti et al., 2003), which contributes to their selection of productive heterogeneous landscapes and edge (Hamer and Herrero, 1987; Robbins et al., 2004; Nielsen et al., 2004a). Given the importance of food and human-caused mortality for bear populations, we advocate that habitat models be used that are based explicitly on trade-offs between resource abundance (foods, nutrition, and energy) and survival.

The application of food and risk-based definitions of habitat is similar philosophically to Cumulative Effects Models (CEMs) and habitat suitability models used for grizzly bear management and conservation during the 1980s and 1990s (Christensen and Madel, 1982; Weaver et al., 1986; Mattson and Knight, 1991; Dixon, 1997; Gibeau, 1998) and subsequent work by Mattson and colleagues in Yellowstone National Park on coefficients of productivity (Mattson et al., 2004). Here the focus was on understanding habitat productivity (food resources) and displacement caused by human developments and human activity (i.e., habitat suitability) rather than habitat selection, which has been the focus of recent telemetry-based definitions of habitat.

In this paper we show how a simple diet-based habitat model based on known distribution of food resource patches, seasonal diets and regional patterns of mortality risk can be used to identify spatially and temporally dynamic patterns of habitat quality without the need of invasive (Cattet et al., 2008) and costly animal capture and collaring approaches now commonly used. We examine how such models relate to local and regional patterns of habitat use and abundance and how maps of potential and realized habitat can help prioritize habitat restoration for managing population recovery.

2. Materials and methods

2.1. A resource-based habitat model

We define potential (resource-based) habitat quality for any particular time period and place as the sum of weighted resource items,

$$pHQ_{ijk} = \sum_{m=1}^n (R_m \times w_m),$$

where potential habitat quality for pixel i of ecosystem j during season k (pHQ_{ijk}) is estimated as the sum of the product between resource abundance R for the m th resource item and a seasonal importance weight w for the same resource item (Fig. 1). Resources would represent food items and measured as the abundance within a study pixel (presence, density, biomass, etc.), while importance weights that may vary by ecosystem would represent the seasonal significance of the food item, such as nutritional value (e.g., digestibility, energy, diet contribution, etc.). When biomass or digestible energy is considered on a per animal foraging basis, non-linear relationships (functional responses) may be necessary to recognize that small quantities of a food item might have limited value, while satiation at high quantities may limit its value to an individual animal during any one particular foraging bout. Across the population of animals and over the time period of interest, however, satiation effects may be less of a concern. In the simplest situation involving a single ecosystem (a region over which a population has similar diets), potential habitat quality for any particular site would be esti-

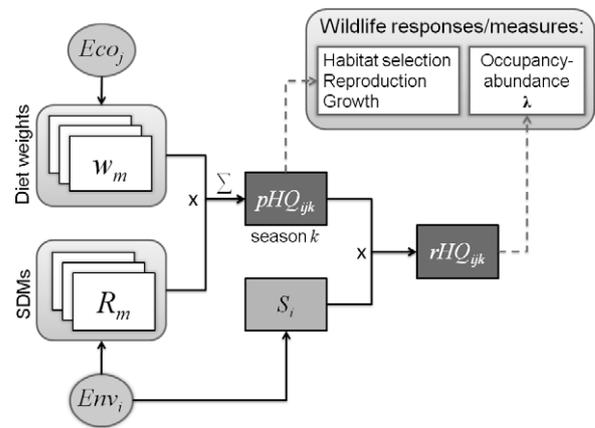


Fig. 1. Cartographic model illustrating the steps used to estimate potential habitat quality (pHQ) and realised habitat quality (rHQ) from species distribution models (SDMs) for m resource items (R_m) based on environmental conditions at site i (Env_i) and field plot information, seasonal (k) diet weights for each resource items (w_m) by ecosystem j (Eco_j) and patterns of survival (S_i). Expected wildlife responses to changes in potential and realised habitat quality shown in upper right of figure.

mated from a single list of food items, their predicted distribution (resource patches) and/or abundance, and a matrix of seasonal importance weights by resource item. To estimate an annual index of potential habitat quality, seasonal habitat quality values would be summed or more formally estimated as,

$$pHQ_{ij} = \sum_{k=1}^n \sum_{m=1}^n (R_{km} \times w_{km}),$$

where the multi-seasonal potential habitat quality value for pixel i of ecosystem j (pHQ_{ij}) is estimated as the sum of the product between resource abundance R in pixel i of ecosystem j for the m th resource item during the k th season and an importance weight w assigned to pixel i of ecosystem j for the same m th resource item and k th season.

Realised habitat quality (rHQ_{ijk}) is estimated as the product between bottom-up regulating factors measured as potential habitat quality (pHQ_{ijk}) at a site and top-down limitations of populations measured through survival or relative mortality risk (Fig. 1).

2.2. A habitat model for grizzly bears

We applied our habitat model to a population of grizzly bears in west-central Alberta, Canada (Fig. 2). Resource abundance (R) was defined by the presence-absence (1 or 0) of resource (food) items (m) in pixel i of our study area based on foods identified to be important in a diet assessment for the population (Munro et al., 2006) and species distribution models for each resource item. Importance weights (w) for each resource item in any one of 10 bi-monthly seasons (k), starting the first two weeks of May and ending on the last two weeks of September, were based on percent digestible dry matter reported in Munro et al. (2006). Percent digestible dry matter is the percent volume of foods in the fecal samples adjusted by a correction factor from Hewitt and Robbins (1996) to account for actual digestible matter and biases in recognizing different fecal residue. Although the use of percent digestible dry matter reduces biases associated with ranking the importance of within-season food items, it cannot be used to rank inter-seasonal differences in the value of food items since the annual index treats each season equally. Use of nutritional quality metrics as weights would overcome this limitation. Because diets varied among mountain and foothill ecosystems (j), we used natural region boundaries (Natural Regions Committee, 2006) to define

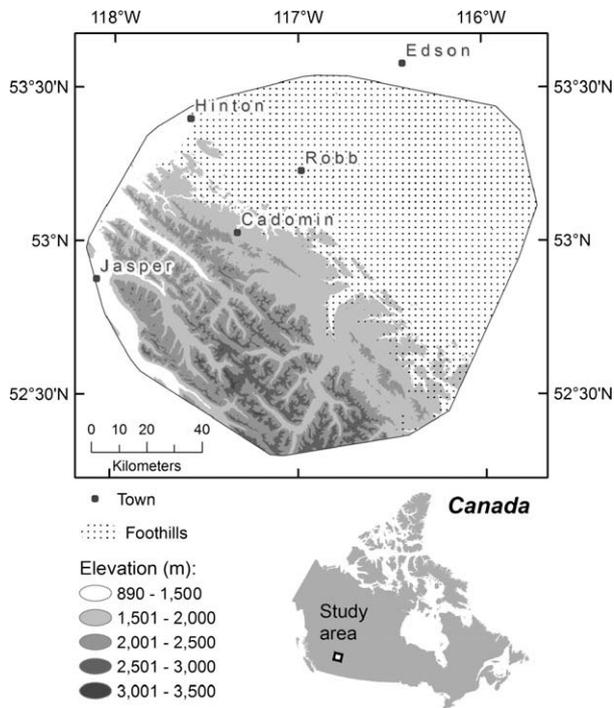


Fig. 2. Study area depicting elevation, towns, Foothills (stippling) and Rocky Mountain (non-stippled area) natural regions.

study pixels as either mountainous or foothills (Fig. 2). Although 40 total food items exceeding 1% digestible dry matter were identified by Munro et al. (2006), only those items containing at least 5% digestible matter for any particular bi-monthly period and ecosystem were considered resulting in a total of 10 major food resource items representing either root digging, herbivory, frugivory or carnivory (including scavenging and myrmecophagy) feeding activities with each activity associated with a specific time of the year (Table 1). Adjustments of potential habitat quality to realised habitat quality were based on top-down limitations of grizzly populations through regional patterns of human-caused mortality risk.

2.3. Model development

2.3.1. Modelling the distribution of resource patches

Resource patches (presence–absence) for nine of 10 resource items were each predicted for the study area based on data collected at 642 stratified (by landcover) random field plots (details of field methods can be found in Nielsen et al., 2004a), a suite of environmental GIS predictors and logistic regression. All statistical analyses were performed in STATA 9 (Stata Corp., College Station, Texas). Presence–absence models for individual food resources

were estimated separately for three habitat strata (forests, clearcuts, and herbaceous communities) to allow landcover-specific responses. Environmental predictors included landcover type from McDermid et al. (2005), climatic variables hypothesized to relate to critical limiting factors or environmental gradients, terrain-influenced local micro-site conditions and forest stand characteristics (Table 2).

In contrast to plant and insect-based resources that could be modeled from plot (presence–absence) data, ungulate resource patches were modeled with a use-available design (Manly et al., 2002) based on 51 known (field-visited GPS telemetry sites) ungulate carcass (or kill) locations used by grizzly bears and reported in Munro et al. (2006). Ungulate use locations were compared with 5100 random available locations drawn from a 2139-km² area delineating the 99% fixed kernel polygon of all 1032 field-visited GPS telemetry locations of six grizzly bears (the 51 ungulate kill locations is a sub-set of this dataset). For ungulate resources, we examined five environmental predictors (canopy, topographic position, soil wetness, percent clear-cut and percent shrub) for three possible scales ranging from local site conditions (30-m pixel) for canopy to a moose home range (Lynch, 1986) scale of 51.6-km² (4053-m radius moving window) for landcover classes important to moose. An intermediate scale of 51.5 ha (405-m radius moving window) was used for local terrain-related factors of soil wetness (CTI) and topographic position. Moose were chosen because moose was the ungulate species most frequently preyed upon or scavenged by grizzly bears in region (Munro et al., 2006). Ratio of use and available locations were balanced by weighting available locations at 0.01, thus resulting in a sample size of 51 carcass locations and 51 random locations (102 total samples).

Models for each food resource were estimated following the approaches suggested by Hosmer and Lemeshow (2000) with univariate analyses used to rank the importance of individual linear factors or hypothesized non-linear forms and interaction terms. Information theoretic approaches (Burnham and Anderson, 2002) were not considered since all explanatory processes/scales (landcover habitat, climate, stand characteristics and micro-site terrain features) were hypothesized to be important *a priori* and since the goal was to maximize map (food model) predictive accuracy and not test competing hypotheses. In the case of the Hosmer and Lemeshow (2000) model selection approach, the highest-ranked uncorrelated factors were introduced individually in a forward manner until all significant ($p < 0.1$) factors were retained. Model accuracy was evaluated using the receiver operating characteristics (ROC) area under the curve (AUC) measure with AUC values of 0.9 and above representing high model accuracy, 0.7–0.9 good model accuracy, and <0.7 low model accuracy (Swets, 1988; Manel et al., 2001). We used the minimum absolute difference between sensitivity and specificity values to estimate an optimal cut-off probability for classifying presence–absence of individual food resource patches (Liu et al., 2005). Resource patches (30-m pixel) for all 10 food types were mapped in a

Table 1

Critical food resources used to define habitat in west-central Alberta, Canada. Food resource, abbreviation (code), feeding activity, and general season of use are described.

Food resource (R_m)	Code	Feeding activity	Season of use
<i>Equisetum</i> spp. (horsetail)	EQAR	Grazing-herbivory	Spring
Forbs	FORB	Grazing-herbivory	Spring–summer
Graminoids	GRAS	Grazing-herbivory	Spring–summer
<i>Hedysarum alpinum</i> (sweet vetch)	HEDY	Root digging	Spring and fall
<i>Heracleum lanatum</i> (cow-parsnip)	HELA	Grazing-herbivory	Summer
Hymenoptera insects (mostly ants)	HYME	Myrmecophagy	Summer
<i>Shepherdia canadensis</i> (buffaloberry)	SHCA	Frugivory	Late summer–fall
<i>Trifolium</i> spp. (clover)	TRRE	Grazing-herbivory	Spring–summer
Ungulate carcass (scavenging or kill site)	UNGL	Carnivory/scavenging	Spring–early summer
<i>Vaccinium membranaceum</i> (huckleberry)	VAME	Frugivory	Late summer and fall

Table 2
Description and characteristics of environmental variables used to model the probability of occurrence of individual grizzly bear food resources in west-central Alberta, Canada.

Variable group	Variable name	Abbrev.	Res. (m)	Units	Data range
<i>Landcover</i>	Deciduous forest	DFOR	30	Category	0 or 1
	Mixed forest	MFOR	30	Category	0 or 1
	Open conifer forest	OCON	30	Category	0 or 1
	Treed bog	TBOG	30	Category	0 or 1
	Anthropogenic	HUMN	30	Category	0 or 1
	Open bog	OBOG	30	Category	0 or 1
	Shrub	SHRB	30	Category	0 or 1
	Clear-cut (regenerating forest)	CUT	30	Category	0 or 1
<i>Climate</i>	Annual moisture index	AMI	500	Unitless	0.29–2.37
	Degree days-base 0 C	DD0	500	Degree days	1134–1918
	Degree days-base 0 C	DD5	500	Degree days	275–1179
	Frost free period	FFP	500	Days	44–87
	Growing season precipitation	GSP	500	mm	308–499
	Mean annual precipitation	MAP	500	mm	483–944
	Mean annual temperature	MAT	500	°C	-2.7–2.8
	Summer moisture index	SMI	500	Unitless	0.57–3.71
<i>Stand conditions</i>	Forest canopy	CNPY	30	Percent	1–100
	Forest age	AGE	30	10 years	0–31.5
	Leaf area index (10 June; 161st day)	LAI-163	30	cm ³ /m ²	0.62–6.01
	Leaf area index (13 August; 225th day)	LAI-223	30	cm ³ /m ²	0.20–9.31
	% Change in LAI (161–225 day)	ΔLAI	30	Percent	-93–328
	Distance to edge	EDGE	30	100 m	0–14.1
<i>Terrain</i>	Compound topographic index	CTI	30	Unitless	3.97–23.5
	Topographic position	TOPO	30	Unitless	-1075–242
	Solar radiation	SOLR	30	kJ/m ² /1000	60.2–91.8

GIS using model estimates. Mapped probabilities were reclassified to binary presence–absence (1 or 0) maps (resource patches) using the cut-off probability estimated from the sensitivity–specificity analysis.

2.3.2. Temporal importance (availability) of resource patches

Seasonal importance weights for each resource item were assigned to each of 10 bi-monthly periods based on seasonal diet patterns corrected to percent digestible dry matter and reported in Munro et al. (2006). We assume digestible matter for individual food items is static over time with changes in the temporal use (availability) of individual food items affecting seasonal changes in the weights. In effect, the seasonal weighting of resource patches resulted in 100 separate spatial–temporal resource patch models (10 resources × 10 seasons). To estimate potential habitat quality, weighted resource patches were summed in a GIS for each bi-monthly period. Annual (multi-seasonal) potential habitat quality was estimated from the sum of seasonal habitat-quality models. In this example, which uses the presence of resource patches and percent digestible dry matter as seasonal importance weights (as opposed to biomass and digestible energy), the annual potential habitat quality index reflects habitat foraging patch use rather than energetic potential since energetic contribution of individual foods vary among seasons.

2.3.3. Estimating realised habitat quality and habitat deficits

At regional scales the patterns of grizzly bear occupancy and abundance are modified by top-down limiting factors based on current and historical patterns of human-caused mortality. Estimates of realised habitat quality must therefore consider tradeoffs with mortality risk (Naves et al., 2003; Nielsen et al., 2004b, 2006). We estimated a model of realised habitat by down-weighting potential habitat quality using a female grizzly bear range occupancy model from Nielsen et al. (2009) that relates to regional source-sink patterns or more broadly top-down limitations of grizzly bear populations due to low survival rates. The female range occurrence

model based on ecosystem type and areas of agriculture predicted the regional distribution (range) of resident adult female grizzly bears, ranging from unoccupied (0) to occupied (1) habitat (Nielsen et al., 2009). Realised habitat quality was estimated as the product between potential habitat quality and probability of regional female grizzly bear range occupancy. Habitat deficits were estimated for the landscape by simply subtracting realised habitat quality from potential habitat quality.

2.4. Model evaluation

2.4.1. Selection of individual food resource patches

We visited 1032 animal use (GPS telemetry) locations of nine sub-adult and adult female grizzly bears in west-central Alberta (Munro et al., 2006) and used these sites to evaluate whether our modeled resource (food) patches could predict the known locations of individual foraging activities for sweet vetch root digging, cow-parsnip herbivory, Hymenoptera insect foraging, frugivory of buffaloberry and carnivory of ungulates. For each foraging item, a logistic regression model was fit that compared known foraging locations for that resource item (1) to a set of random available locations (0) using the predicted probability (or presence) of the resource patch at each site as the explanatory variable. We focused on female bears since this sex–age class has the highest demographic elasticity (Harris et al., 2005) and is thus the focus of most management efforts. Since intra-specific competition with adult males may result in exclusion of sub-dominant animals (including females) from the highest quality resource patches (Egbert and Stokes, 1976; Stringham, 1983), caution should be used during interpretation. Although these data represent an independent assessment of habitat use for plant resources, predictive accuracy may be overestimated for ungulate resources because the same locations were used for model building. Relative selection ratios (i.e., the ratio of probabilities) of the use of predicted resource patches (to random resource use) are reported.

2.4.2. Selection of seasonal habitats

In addition to assessing use of individual food patches, we also used 42,853 GPS telemetry locations from 44 radio-collared grizzly bears to assess the predictive performance of our bi-monthly habitat-quality models. Although not all telemetry locations represent foraging sites, we still expect a positive correlation between potential habitat quality and animal use. To test whether potential habitat quality was positively related to use by bears, seasonal habitat quality at telemetry locations was compared to habitat quality at random landscape locations within the home range for each animal. Habitat availability was estimated within an animal’s multi-annual minimum convex polygon (MCP) home range (design III, Thomas and Taylor, 1990) with a sampling intensity of 1 location per 1-km². Locations of random available samples were kept constant among seasons to ensure that seasonal changes in selection of habitats were due to changes in habitat use and not differences in the method of sampling. Given animal-specific estimates of selection for each of the 10 seasonal periods, population-level seasonal selection (expressed as relative selection ratios) was estimated as the mean of individual animal selection following a two-stage modelling process (Cox and Hinkley, 1974 in Manly et al. (2002)). Population-level significance from individual-based

estimates of selection was estimated using a one-sample *t*-test (H_a : mean > 1).

2.4.3. Realised habitat quality and local patterns of occupancy-abundance

We used data from a late spring-early summer (June–July) DNA mark-recapture hair-snag (Woods et al., 1999) study (8820-km² area of foothills) reported in Boulanger et al. (2005) to estimate regional patterns of occupancy (detected-undetected) and relative abundance (number of unique individuals) of grizzly bears. We used the index of multi-seasonal realised habitat quality to predict occupancy-abundance of bears since local patterns in grizzly bear abundance was predicted to be positively related to both the total amount of seasonal foods available to bears (potential habitat quality) and to top-down limitations of populations due to regional survival patterns. We used a zero-inflated count (Poisson) model (Barry and Welsh, 2002) to relate local occupancy-abundance with realised habitat. The zero-inflated count model assumed two latent groups: group A, the inflation part that only represented excess absent locations (i.e., the absences not predicted by the Poisson part of the model); and group ~A, which represented the counts including zeros (Long and Freese, 2003). A Vuong (*V*) test (Vuong, 1989)

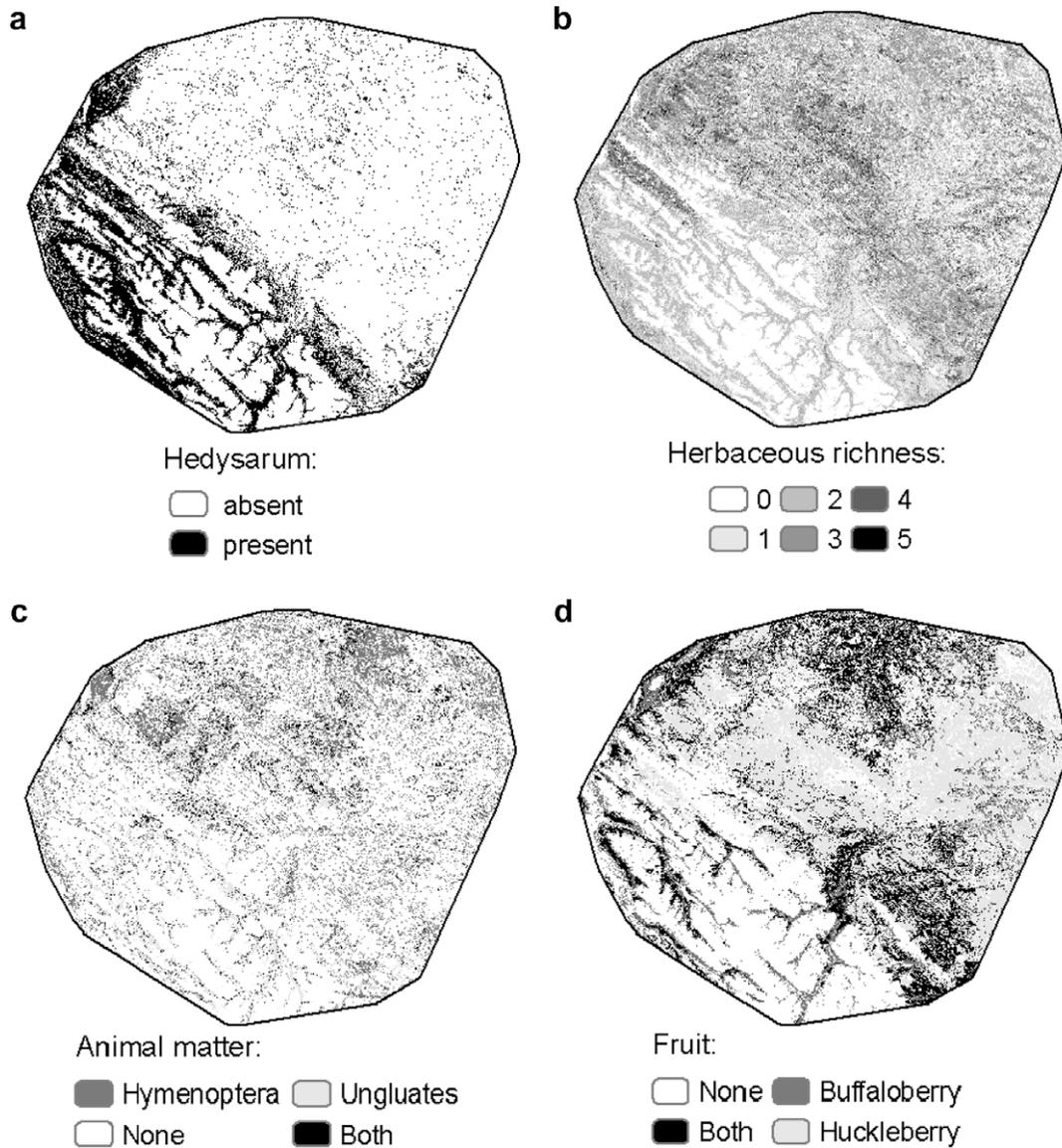


Fig. 3. Predicted distribution of major grizzly bear resource items by foraging type (a: *Hedysarum alpinum* roots; b: herbaceous plant richness; c: animal matter; and d: fruit).

was used to ensure that a zero-inflated count model was necessary, while a spearman rank test between model predictions and observations was used to evaluate within-model predictive accuracy. Because occupancy and abundance are unlikely to be explained by patch-level (30-m pixel) habitat conditions, realised habitat around hair-s snag locations was examined at four possible scales: (1) 300-m radius or 10 times the original map grain; (2) 1.69-km radius or detection scale of hair-s snag sites (Boulanger et al., 2004); (3) 3.95-km radius or the scale of the DNA sampling grid used for locating 're-capture' sites; and (4) 10-km radius or approximately the 90% kernel home range of female grizzly bears in the area (Nielsen et al., 2008).

3. Results

3.1. Distribution of resource food patches

Rooting resources, represented by sweet vetch, were most common to mountain environments, but also represented in riparian habitats and many low elevation disturbed sites in the foothills (Fig. 3a). In forested stands, sweet vetch was more common in open conifer and treed bog stands, and stands with high soil wet-

ness or canopy (Table 3). Herbaceous foods, represented by horse-tails, forbs, graminoids, cow-parsnip and clover, varied in their distribution and response to environmental factors (Tables 3–6), but excluding barren mountains, at least one resource was represented at nearly all sites making it a rather ubiquitous resource (Fig. 3b). Animal matter was predicted to be high in the foothills where Hymenoptera insects were more common, as well as disturbed habitats conditions that favoured moose (Fig. 3c). In forests, Hymenoptera were negatively related to stand age, canopy cover, and soil wetness, although occurrence did increase in wet sites having high canopy coverage (i.e., a positive interaction) and in forests having low or high solar radiation (Table 3). Ungulate carcass locations were positively associated with increasing shrub and moderate clear-cut composition at moose home range scales (i.e., 51.6-km²), intermediate canopy conditions at the site level (30-m pixel) and local (51.5 ha) patterns of high soil wetness and low landscape position (Table 6). Finally, fruiting resources (buffaloberry and black huckleberry) were predicted to occur throughout the forested areas, especially at lower elevations for buffaloberry and moderate to high elevations for black huckleberry (Fig. 3d). Buffaloberry occurrence was positively related to intermediate aged forest stands, areas of high solar radiation and low topo-

Table 3
Estimated coefficients describing the occurrence of nine grizzly bear food resources (see Table 1 for definitions of four letter codes) in non-harvested forest stands near Hinton, Alberta.

Variables	Roots	Herbaceous matter					Animal	Fruit	VAME
	HEDY	EQAR	FORB	GRAS	HELA	TRRE	HYME	SHCA	
<i>Habitat type^a</i>									
DFOR	−0.245	−0.661	2.09	0.712	−1.21	0.898	0.963	0.745	−1.12
MFOR	0.156	0.355	1.04	1.83	−0.154	0.732	0.457	1.88	−0.523
OCON	1.36	−0.149	1.05	0.881	−2.84	2.06	1.07	0.478	−0.577
TBOG	1.10	2.25	1.42	−1.23	None	0.646	0.899	−1.77	None
<i>Climate</i>									
AMI			−1.01						
DDO	−0.073								
DDO ²	0.235 ^c								
FFP	−0.145				5.735	2.17			
FFP ²					−0.041	−0.016			
GSP				−0.017				0.406	0.046
GSP ²								−0.551 ^b	
MAT		0.77							
MAT ²		−0.297							
<i>Stand conditions</i>									
AGE			−0.076				−0.094	0.536	
AGE ²								−0.032	
CNPY	0.818	0.757		−0.352			−0.488		
EDGE						−1.123			
LAI-161			−3.37	−2.87					
LAI-161 ²			0.448	0.474					
LAI-225					0.604				2.78
LAI-225 ²									−0.259
ΔLAI									−0.033
<i>Terrain</i>									
CTI	0.297	0.552			−1.12		−0.323		
CTI ²					0.055				
SOLR				−11.3	−3.74		−0.873	0.233	
SOLR ²				0.069	0.024		0.006		
TOPO								−0.005	
<i>Interactions</i>									
CTI × canopy	−0.091	−0.093					0.052		
Constant	59.1	−5.8	10	478.4	−58.9	−74	34.9	−95.4	−28.3
<i>Model evaluation</i>									
LR χ^2	78.1 [*]	54.7 [*]	39.1 [*]	60.8 [*]	41.1 [*]	20.3 [*]	41.8 [*]	109.4 [*]	31.5 [*]
ROC	0.888	0.730	0.729	0.846	0.877	0.867	0.726	0.877	0.789
Cut-off prob.	0.163	0.294	0.710	0.788	0.051	0.062	0.335	0.253	0.144

^a Closed conifer used as reference category in indicator contrasts of forest habitat types.

^b Coefficients 1000 times their original value.

^c Coefficients 10,000 times their original value.

^{*} Significant at the $p < 0.01$ level.

graphic position, while black huckleberry occurred in forests (especially closed conifer stands) with higher growing season precipitation (Table 3). Likelihood ratio model χ^2 statistics and ROC AUC results indicated that all resource patch models were significant and all but forbs and clover in harvested forests had 'good' (ROC AUC of 0.7–0.9) to 'high' (ROC AUC >0.9) predictive accuracy (Tables 3–5).

3.2. Selection of individual food resource patches

Patches of sweet vetch, cow-parsnip, Hymenoptera and buffaloberry were all used more than random at relative selection ratios of 2.4, 1.9, 2.1, 5.2, and 8.7 times respectively (Table 7). All models were significant except cow-parsnip, which likely reflects the small number of documented cow-parsnip feeding sites used for assessment ($n = 25$). When using probability of occurrence for individual food resources (versus predictions of presence-absence), all models were significant, including cow-parsnip, with relative selection ranging from a low of 7.0 (SE = 1.8, $p < 0.001$) for Hymenoptera insects to a high of 68.9 (SE = 41.8, $p < 0.001$) for ungulate carcass sites (Table 7).

3.3. Seasonal habitat-quality models

Potential habitat quality varied spatially and temporally (bi-monthly) reflecting wide-spread differences in the distribution of food resources and temporal changes in grizzly bear diets (Fig. 4). Considering multi-seasonal habitat quality, potential habitat quality was highest in low elevation mountain valleys and young forest stands in the upper foothills (Fig. 4d). Despite high values in mountain valleys, much of the Rocky Mountain region

was non-vegetated (38.3% of alpine/sub-alpine and 11.6% of montane vs. 3% for the foothills) reducing overall habitat conditions for the natural region. Few sites (pixels) contained all possible resource items reducing multi-seasonal habitat quality well below the possible maximum (Fig. 4d).

3.4. Selection of seasonal habitats

Seasonal telemetry locations of grizzly bears were positively related to potential habitat quality, although strength of relationships were highest during the mid-summer to late-summer periods (late July and early August) when diets shifted from herbivory to frugivory (Fig. 5). Relative selection ratios (per standard deviation increase in habitat quality) of high-quality habitats compared with random home range locations ranged from a low of 1.3 in early May and early September to 1.6 during early August (Fig. 5). Assuming a three standard deviation increase in habitat quality, bears would be predicted to increase use by a factor of 4–5. No significant differences between sexes were found. Reporting potential habitat quality by landcover type, open conifer had the highest average potential habitat quality at 53.5%, while treed bog had the lowest average potential habitat quality at 19.3% (Fig. 7).

3.5. Realised habitats and habitat deficits

Realised habitat was highest in sub-alpine valleys and lowest in the lower foothills (Fig. 6a). Considering displacement of historic grizzly bear populations from resource-rich habitats, estimated habitat deficit (absolute habitat loss) was highest in the montane region of the Rocky Mountains (Fig. 6b). Open conifer had the high-

Table 4

Estimated coefficients describing the occurrence of nine grizzly bear food resources (see Table 1 for definitions of four letter codes) in harvested forest stands near Hinton, Alberta.

Variables	Roots	Herbaceous matter					Animal	Fruit	
	HEDY	EQAR	FORB	GRAS	HELA	TRRE	HYME	SHCA	VAME
<i>Climate</i>									
AMI								10.6	-46.2
AMI ²									13.8
DD0	-0.293		-0.006						
DD0 ²	0.112 ^a								
DD5		0.096							
DD5 ²		-0.493 ^b							
FFP			-1.83				-0.115	-2.14	
FFP ²			0.013					0.016	
GSP	-0.061								
MAP				0.868		-0.506			
MAP ²				-0.707 ^a		0.415 ^a			
<i>Stand conditions</i>									
AGE		-1.29	0.214				2.58		
AGE ²		0.140					-0.487		
LAI-161								0.943	13.8
LAI-161 ²									-1.73
LAI-225							1.17		
LAI-225 ²							-0.123		
ΔLAI						0.014			
<i>Terrain</i>									
CTI	0.382			-12.7					
CTI ²				0.744		0.209			
SOLR					0.294				-0.140
TOPO	-0.014	-0.200			0.045				
TOPO ²					0.181 ^a				
Constant	211	-45.1	73.1	-209	-28.9	149.8	4.21	44.9	20.6
<i>Model evaluation</i>									
LR χ^2	62.3 [*]	48.0 [*]	19.1 [*]	16.3 [*]	14.0 [*]	19.5 [*]	48.0 [*]	39.0 [*]	19.6 [*]
ROC	0.938	0.754	0.682	0.872	0.718	0.675	0.738	0.872	0.788
Cut-off prob.	0.108	0.415	0.699	0.950	0.026	0.138	0.661	0.11	0.076

^a Coefficients 1000 times their original value.

^b Coefficients 10,000 times their original value.

^{*} Significant at the $p < 0.01$ level.

Table 5

Estimated coefficients describing the occurrence of six grizzly bear food resources (see Table 1 for definitions of the four letter codes) for herbaceous open habitats near Hinton, Alberta. Forbs occurred in every open habitat type (ubiquitous presence), while HELA and VAME were absent from all open sites.

Variables	Roots	Herbaceous matter			Animal	Fruit
	HEDY	EQAR	GRAS	TRRE	HYME	SHCA
<i>Habitat type^a</i>						
HUMN	-2.32	0.842	All	0.056	-1.29	2.81
OBOG	None	1.17	-3.03	None	-0.977	0.562
SHRB	0.130	0.360	-1.26	None	-1.81	None
<i>Climate</i>						
DDO						-0.017
DD5		0.002				
MAT	0.559					
SMI				25.9	12.3	
SMI ²				-5.81	-2.72	
<i>Stand conditions</i>						
EDGE					-0.919	
LAI-225			0.543		-1.74	-3.14
LAI-225 ²					0.256	0.308
ΔLAI	0.028					
<i>Terrain</i>						
CTI	-1.034	0.136				
CTI ²	0.044					
SOLR					-2.98	-0.412
SOLR ²					0.020	
TOPO					0.006	
TOPO ²					0.076 ^b	
Constant	2.72	-3.96	0.699	-28.8	102	60.6
<i>Model evaluation</i>						
LR χ^2	24.0*	22.4*	14.4*	25.1*	44.8*	15.3*
ROC	0.889	0.770	0.822	0.905	0.874	0.904
Cut-off prob.	0.211	0.390	0.790	0.355	0.405	0.089

^a Herbaceous openings used as reference category in indicator contrasts of habitat types.

^b Coefficients 1000 times their original value.

* Significant at the $p < 0.01$ level.

Table 6

Ungulate carcass (kill site) model (LR $\chi^2 = 37.0$, $p < 0.001$, $DF = 7$) describing the relative probability of a site being classified as an ungulate (primarily moose) kill location (optimal cut-off probability of 0.5497). Model accuracy was good (AUC = 0.823) with excellent model fit (Hosmer and Lemeshow GOF $\chi^2 = 112.63$, $p = 1.0$).

Variable	Scale	Coef.	SE	p
CNPY	30-m pixel	0.097	0.043	0.025
CNPY ²	30-m pixel	-0.010	0.005	0.034
TOPO	51.5 ha	-0.019	0.162	0.002
CTI	51.5 ha	0.311	5.295	0.056
CUT (%)	51.6-km ²	0.143	0.103	0.007
CUT ²	51.6-km ²	-0.260	0.055	0.012
SHRB (%)	51.6-km ²	0.154	0.055	0.005
Constant	NA	-6.859	1.925	<0.001

Table 7

Predictive performance of individual resource models for predicting foraging activity of nine grizzly bears (odds ratio) compared to random available locations. Number (n) of field-visited telemetry observations with food resource use documented is reported.

Food resource	n	Prob. of occurrence			Presence-absence		
		Odds ratio	SE	p	Odds ratio	SE	p
Sweet vetch (HEDY)	253	7.3	2.0	<0.001	2.4	0.4	<0.001
Cow-parsnip (HELA)	25	12.2	14.3	0.030	1.9	0.8	0.115
Hymenoptera (HYME)	204	7.0	1.8	<0.001	2.1	0.3	<0.001
Buffaloberry (SHCA)	82	15.6	5.4	<0.001	5.2	1.2	<0.001
Ungulate carcass/kill site (UNGL)	51	68.9	41.8	<0.001	8.7	2.9	<0.001

est average realised habitat quality, while treed bog had the lowest average realised habitat quality (Fig. 7). Habitat deficits were most pronounced for landcover types common to the montane and lower foothills region. In particular, deciduous and mixed forests had the most substantial losses due to the diversity of grizzly bear foods in these stands and their location at lower elevations. Closed conifer, on the other hand was the most stable landcover type due to the general scarcity of grizzly bear foods (Fig. 7).

3.6. Realised habitat quality and local patterns of occupancy-abundance

Realised habitat quality predicted patterns of occupancy-abundance (LR $\chi^2 = 7.84$, $p = 0.005$) with local (300-m) averages of realised habitat quality best predicting occupancy and average realised habitat quality at regional home range sized areas (10-km) best predicting relative abundance of bears at hair-snag sites (Table 8). Specifically, for each standard deviation increase in realised habitat quality, there was a 81% ($\pm 13\%$) increase in occupancy and a 32% ($\pm 12\%$) increase in grizzly bear abundances predicted (Table 8). A significant Vuong test ($V = 6.02$, $p < 0.001$) confirmed the need for a zero-inflated process, while a spearman rank correlation of model predictions and observations confirmed good within-model predictive accuracy ($r_s = 0.219$, $p < 0.001$), including only those locations where bears were present ($r_s = 0.252$, $p = 0.043$).

4. Discussion

Grizzly bears are especially well suited to food-based definitions of habitat, because they have a diverse and omnivorous diet that affects body condition (Pritchard and Robbins, 1990; Hilderbrand et al., 1999a; Rode et al., 2001) and population density (Hilderbrand et al., 1999b). Resource selection functions (RSFs, Manly et al., 2002), facilitated by geographic information systems (GIS) and advances in telemetry, have been used extensively over the past decade to model habitat conditions for bears (e.g., Mace et al., 1999; McLellan and Hovey, 2001; Nielsen et al., 2003, 2004c, 2006; Ciarniello et al., 2007a, 2007b). RSFs, however, have most often estimated habitat selection using surrogate habitat variables for which spatial data readily exist (e.g., remote sensing, digital elevation maps and vegetation inventories). Although predicting habitat use/selection reasonably well (Boyce et al., 2002), the use of such surrogates seldom reveal the mechanisms for habitat selection and have not been directly related to population performance or the health of individuals. Behaviour of animals is also often ignored resulting in predictions of habitat use that despite being predictive may not represent critical habitat needs. For instance in many species, including bears, bedding/resting locations often occur in separate habitats from foraging locations (e.g., Munro et al., 2006) with no indication that bedding/resting habitats limit population number or growth or the health of individual animals. Inclusion of such locations within RSF models is therefore likely to attenuate descriptions of habitat quality, despite main-

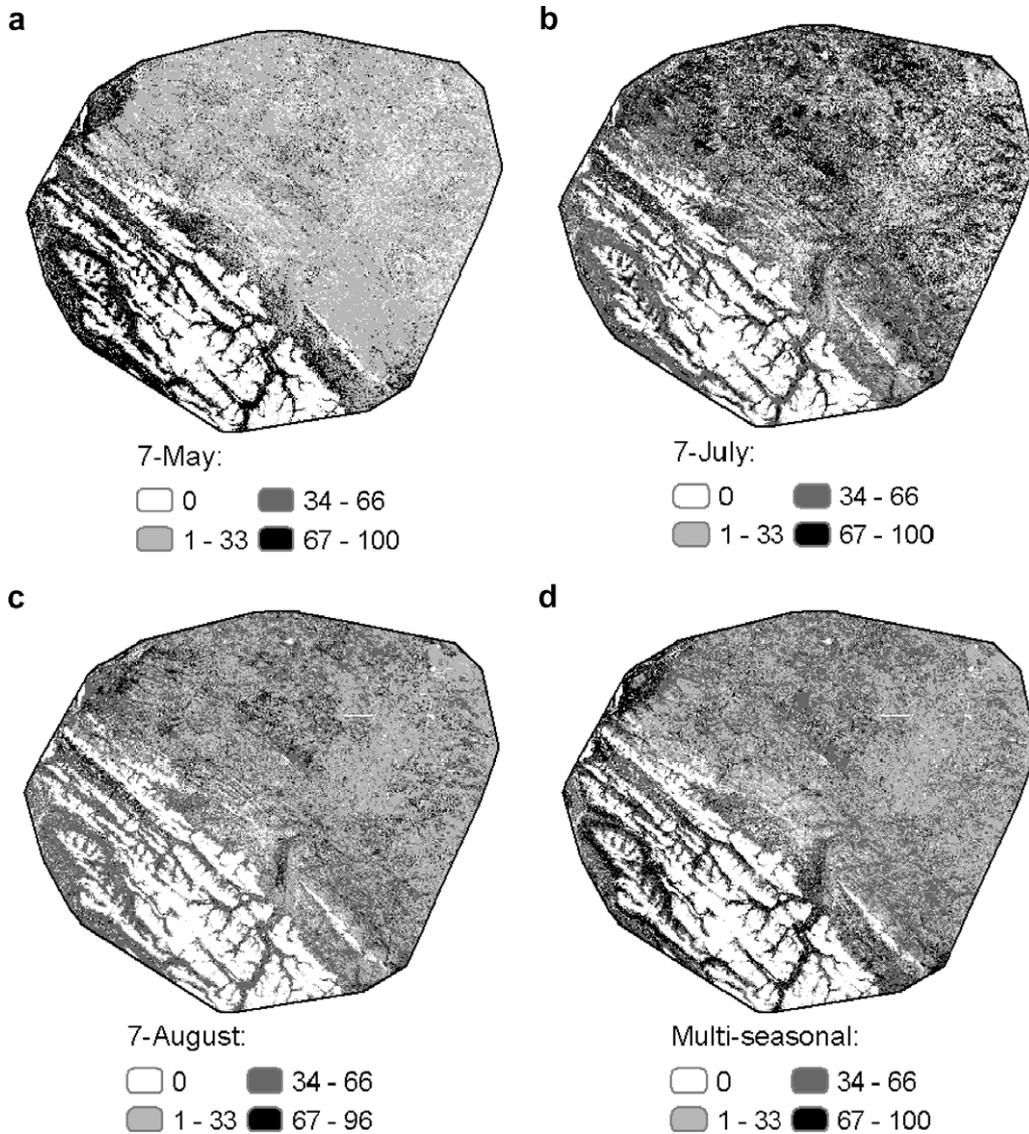


Fig. 4. Example bi-monthly (a: 7 May; b: 7 July; c: 7 August) and multi-seasonal (d: 1 May–31 September expressed as % of total possible) potential habitat quality.

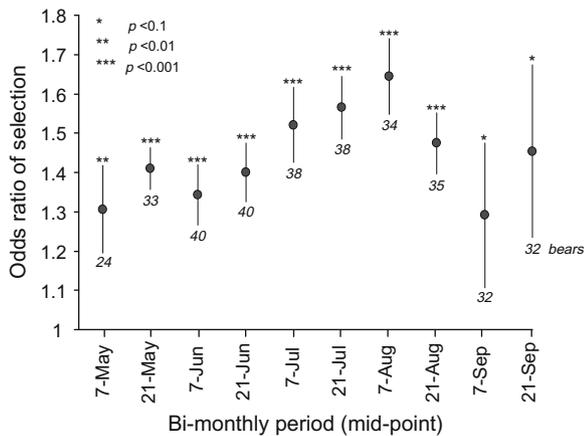


Fig. 5. Mean (\pm SE) seasonal (bi-monthly) selection expressed as odds ratios (relative selection) for a 1 unit standard deviation increase in potential habitat quality. Significance of bi-monthly periods based on a one-sample *t*-test (H_a : mean > 1). Number of bears tested in each season indicated below seasonal point estimates.

taining excellent predictive accuracy for measures of habitat use and selection. Even when locations are restricted to foraging locations there is the concern that foraging habitats that are selected in areas of high human activity would result in a habitat (ecological) trap situation due to increased risk of mortality not perceived by the animals (Nielsen et al., 2006). Measures of habitat use and selection alone would in such cases result in improper definitions of habitat quality. Consideration of survival is therefore needed (Johnson et al., 2004; Nielsen et al., 2004b, 2006).

To address some of these limitations, we describe a generalized approach for measuring and mapping habitat quality that focuses on tradeoffs in food resource abundance and survival. Our approach is similar philosophically to the habitat effectiveness and cumulative effects modelling once common decade's earlier (Christensen and Madel, 1982; Weaver et al., 1986; Mattson and Knight, 1991; Dixon, 1997; Gibeau, 1998) and more recently described in units of digestible energy by Mattson et al. (2004) in Yellowstone National Park. The assumption with this approach is that both bottom-up (food resource abundance) and top-down (human-caused mortality) factors regulate or limit grizzly bear populations by influencing individual health (e.g., body mass), habitat-based carrying capacity, fecundity, and survival (Naves et al., 2003). The

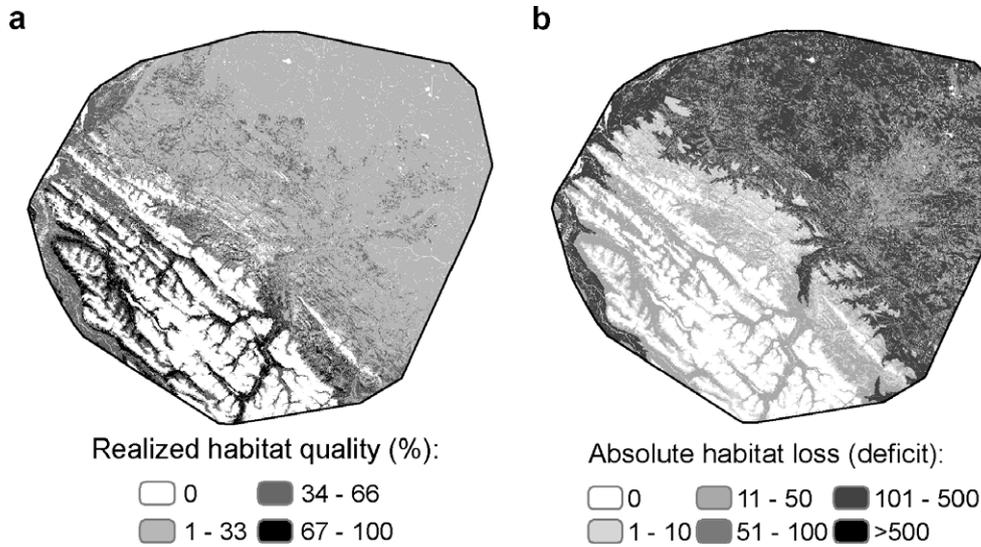


Fig. 6. Patterns of multi-seasonal realised habitat quality (a) and habitat deficit (b).

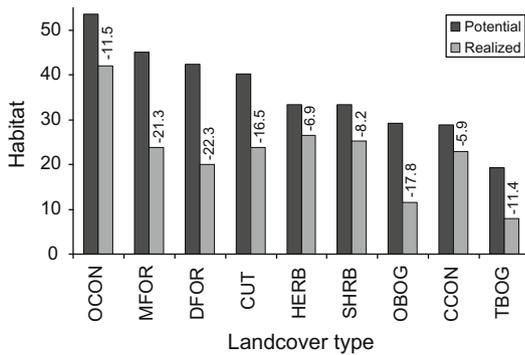


Fig. 7. Average realised and potential multi-seasonal habitat quality (% of total) by landcover type (see Table 2 for landcover codes). Habitat deficits (in absolute terms) reported above realised habitat landcover categories.

Table 8

Zero-inflated Poisson model results evaluating the relationship between realised habitat quality (measured as standard deviation changes) and occupancy-abundance of grizzly bears at hair-snag locations in west-central Alberta, Canada.

Variable (scale)	Group A (zeros)			Group ~A (counts)		
	Coef.	SE	<i>p</i>	Coef.	SE	<i>p</i>
<i>rHQ</i> (300-m)	0.813	0.132	<0.001			
<i>rHQ</i> (10-km)				0.318	0.115	0.006
Constant	2.447	0.170	<0.001	0.736	0.128	<0.001

use of surrogate habitat variables and habitat selection analyses has not resulted in substantial gains in managing bottom-up processes despite gains in managing top-down factors (restrictions in human access and road decommissioning). Once access management and education programs to reduce bear-human conflict are in place, management of recovering bear populations should consider actions that benefit habitat productivity, such as forest silvicultural practices that enhance and prolong the period of fruit production and root, insect and ungulate populations (Nielsen et al., 2004a). Recommendations of specific management actions, however, are generally not possible when using habitat selection analyses that rely on surrogate habitat variables.

Our approach to defining bottom-up resources rests upon the knowledge of seasonal diets of grizzly bears that are already

well-described for many populations of bears (e.g., Hamer and Herero, 1987; McLellan and Hovey, 1995; Munro et al., 2006). Diet studies alone, however, cannot describe spatial patterns of habitat quality at the scales which land management and conservation planning occur. Knowledge of food resource distribution, abundance, and nutritional quality at these same scales is therefore also needed. We used species distribution models based on information from vegetation field plots to estimate the location of important food patches (Nielsen et al., 2003) and weighted those patches based on percent digestible dry matter from a diet study (Munro et al., 2006). Although we used resource patches defined by the presence-absence of food items to measure resource availability, actual abundance (density or grams of resource), or better yet resource nutrition (e.g., starch, protein, and carbohydrate) and energetics (e.g., kilocalories or potential net digestible energy) should be considered to facilitate accurate comparisons among seasonal habitat conditions and overall multi-seasonal estimates of habitat quality. Early work in cumulative effects modelling suffered from the inability to properly scale seasonal habitat models for comparison. Spatially quantifying net digestible energy across a landscape, which was the approach used by Mattson et al. (2004) for land cover types in Yellowstone, would solve this problem.

Despite lacking direct energetic-based predictions (e.g., Mattson et al., 2004), we successfully predicted the locations of radio-collared grizzly bears based solely on knowledge of seasonal diets and the location of food resource patches. Population measures of occupancy-abundance at local hair-snag sites, however, necessitated that regional survival patterns be considered with resource models. This suggests that the low overall population densities observed in the area are due not only to high rates of human-caused mortality, but also bottom-up regulating processes associated with patterns of food resource abundance. By mapping differences in potential and realised habitat quality we estimated areas and amount of habitat deficit, which provided a useful metric from which to understand top-down limiting factors and for targeting the most effective habitat restoration efforts, such as road gating, road closures and decommissioning of roads (Noss et al., 2009). Functional habitats with both the highest potential and realised conditions were open conifer stands, while mixed and deciduous forests were characterized by having the highest habitat deficits suggesting that the greatest gains in restoration through access management would be in the deciduous and mixed forest sites. Conversely, open conifer stands should be considered a priority

for maintenance and protection given their high potential and realised habitat quality.

5. Conclusion

Recent technological advances in telemetry (i.e., global positioning systems) and increased availability and management of spatially-explicit information (i.e., GIS and associated spatial databases) have profoundly changed wildlife research, often for the better. However, as with any technology its overreliance to the exclusion of other forms of information and questioning can result in a technology trap. Results can be produced quickly, but often with limited biological information, interpretability and management application. Wildlife habitat models, such as RSFs (Manly et al., 2002), have increased dramatically in popularity over the past decade, despite few if any demonstrated linkages to demographic processes or direct measures of regulating factors of populations (Nielsen et al., 2005; Johnson and Seip, 2008). Rather than searching for habitat selection patterns with indirect resource gradients that are often static in nature, we suggest that more attention be given to spatial-temporal patterns in food resources affecting bottom-up regulation of populations, while top-down limitations of populations be integrated into wildlife habitat models through survival or relative differences in mortality risk. Such an approach is necessary for understanding and accurately predicting the effects of changing environments on populations.

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