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A habitat-based framework for grizzly bear conservation in Alberta

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Grizzly bear (*Ursus arctos* L.) populations in Alberta are threatened by habitat loss and high rates of human-caused mortality. Spatial depictions of fitness would greatly improve management and conservation action. We are currently challenged, however, in our ability to parameterize demographic rates necessary for describing fitness, especially across gradients of human disturbance and for land cover types. Alternative approaches are therefore needed. We describe here a method of estimating relative habitat states and conditions as surrogates of fitness using models of occupancy and mortality risk. By combining occurrence and risk models into a two-dimensional habitat framework, we identified indices of attractive sinks and safe harbour habitats, as well as five habitat states: non-critical habitats, secondary habitats (low-quality and secure), primary habitats (high-quality and secure), secondary sinks (low-quality, but high risk), and primary sinks (high-quality and high risk). Primary sink or high attractive sink situations were evident in the foothills where bears were using forest edges associated with forestry and oil and gas activities on Crown lands, while primary habitats or safe harbour sites were most common to protected alpine/sub-alpine sites. We suggest that habitat states and indices be used for setting baseline conditions for management and comparison of habitat conditions over time and identification of grizzly bear conservation reserves. A no net loss policy of critical habitats could be used to maintain existing habitat conditions for landscapes threatened by human development. Under such a policy, conversions of primary habitat would require restoration of equivalent amounts of primary sinks through decommissioning of roads.

1. Introduction

Understanding the distribution and abundance of species in space and time is the primary definition of ecology (Krebs, 1985). With the recent advent of geographic information systems (GIS), together with widespread availability of digital geo-spatial data, predicting species occurrence and/or abundance has become commonplace (Boyce and McDonald, 1999; Scott et al., 2001). Applications of such models include climate-change assessments (Tellez-Valdes and Davila-Aranda, 2003), restoration or range expansion (Mladenoff et al., 1995; Boyce and Waller, 2003), ecological risk assessment (McDonald and McDonald, 2002), and conservation gaps or reserve design (Flather et al., 1998; Yip et al., 2004). Ultimately, understanding large-scale patterns and temporal changes to rare, threatened or endangered species helps focus conservation needs (Dobson et al., 1996; Mattson and Merrill, 2002).

Describing species occurrence, or even that of abundance, however, does not necessarily parallel habitat relationships for populations, as occurrence and abundance can be poor

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surrogates for demographic performance (Van Horne, 1983; Hobbs and Hanley, 1990; Tyre et al., 2001). Relating life history traits to habitats is critical for understanding habitat processes and ultimately the management of species of conservation concern (Franklin et al., 2000; Breininger and Carter, 2003). Without understanding such functions, one risks assuming that animal occurrence or abundance relates directly to habitat quality, something that is not always the case. For instance, some sites considered high in habitat quality from an occupancy standpoint may be low in survival and/or final recruitment. These 'attractive' habitat patches can produce local population sinks, and therefore have been called attractive sinks (Delibes et al., 2001; Naves et al., 2003) or ecological traps (Dwernychuk and Boag, 1972; Ratti and Reese, 1988; Donovan and Thompson, 2001). Recognizing this phenomenon within conservation habitat models and resulting planning maps is therefore crucial for fully representing habitat quality. For many species, however, we lack the necessary data to formulate habitat-specific demographic parameters and waiting for such data to be collected for long-lived species with low reproductive rates might simply result in documenting the decline rather than providing an initial recommendation for the conservation problem. No doubt, collection of long-term life history information needs to be gathered, but exploiting existing data sources also is necessary for short-term conservation management. Commonly, what is available is information on animal occupancy from aerial surveys or radiotelemetry studies and sometimes a distribution of mortality locations from government management databases (e.g., hunting, problem wildlife, vehicle-wildlife collisions, etc.). Identifying attractive sink habitats, as well as some form of source or secure habitats from these data, would prove useful for conservation planning and wildlife management.

One species ideally suited for exploring conservation habitat modelling from an occupancy and survival framework is grizzly bears *Ursus arctos* L. Grizzly bears are an important keystone species (Tardiff and Stanford, 1998) that have declined substantially throughout much of North America in the past century (McLellan, 1998; Mattson and Merrill, 2002), largely due to vulnerability from late maturation, low density, low reproductive rates and a high trophic level (Russell et al., 1998; Purvis et al., 2000a,b; Woodruffe, 2000; Garshelis et al., 2005). Current efforts to identify grizzly bear habitats have relied on radiotelemetry analyses of habitat selection (Waller and Mace, 1997; Mace et al., 1996, 1999; McLellan and Hovey, 2001; Nielsen et al., 2002, 2003) or assessments of occupancy based on field surveys and published records (Naves et al., 2003; Posillico et al., 2004). Resulting habitat models provide assessments of animal occurrence or use, but cannot suggest overall habitat quality based on demographic performance. Even spatial models that predict grizzly bear abundance (Apps et al., 2004), although adding additional information over and above occupancy and use, still lack an explicit mechanism to identify conservation actions. What is needed is an approach that merges habitat-related occurrence or animal abundance models with critical life history parameters.

For grizzly bears, it is widely accepted that survival, especially that of females, is the most sensitive parameter for population growth (Knight and Eberhardt, 1985; Mattson et al., 1996; Wiegand et al., 1998; Boyce et al., 2001; Wielgus et al., 2001). Most grizzly bear mortalities are human-caused (McLellan et al., 1999; Benn and Herrero, 2002) and related to human access (Nielsen et al., 2004a). Incorporating some form of survival within habitat maps would therefore be helpful. Although population-level estimates of survival have been estimated for grizzly bears (e.g., McLellan et al., 1999), few have attempted to define or index these in a spatial manner necessary for targeting on-the-ground management (see however, Nielsen et al., 2004a; Johnson et al., 2004). Recently, Naves et al. (2003) used a spatial framework for defining brown bear habitats in northern Spain that incorporated both survival and reproduction simultaneously. Such modelling and mapping approaches are attractive management tools for identifying conservation needs because they record attractive sinks where animals are likely to be present, but suffer high mortality rates, and source or secure habitats where animals are present and enjoy high survival. Both habitat states provide managers with 2 separate conservation strategies: (1) preservation and protection of existing source and secure areas to impede habitat degradation; and (2) mitigation of sites where habitat conditions are excellent, but risk of mortality is high and manageable.

Here, we develop a framework for identifying attractive sink and source-like habitats for grizzly bears in west-central Alberta, Canada. Such an approach is especially warranted for this region, given the recommendation of threatened status by Alberta's Endangered Species Conservation Committee (Stenhouse et al., 2003). With any such change in status, effective habitat maps will be necessary for appropriate management and conservation planning. Despite the recognition of population declines and the importance of secure habitats, current management is largely based on a 1988 assessment of land cover and human disturbance (Stenhouse et al., 2003). We propose to update this assessment and redefine grizzly bear habitat using empirical models of animal occurrence and risk of human-caused mortality specific to current conditions in the east slopes of the Alberta Rocky Mountains. By placing occupancy and mortality risk models in a two-dimensional framework, we define indices of attractive sink and safe-harbour (source-like or secure) habitats as well as a classification of 5 habitat states including, non-critical habitat, secondary sink, primary sink (similar to high index values of attractive sink habitats), secondary habitat, and primary habitat (similar to high index values safe harbour habitats). Although these habitat indices and states are not based directly on demographic parameters, they have value in tracking temporal changes in habitats and ranking areas for conservation action.

2. Study area

Our 9,752-km^2-study landscape was located in west-central Alberta, Canada (53° 15′ N 118° 30′ W; Fig. 1). Two land use zones dominated the region: (1) the protected mountains in the west, and (2) the resource-utilized foothills in the east. Management of the protected mountains were divided between provincial (i.e., Whitehorse Wildlands; 173-km^2) and federal (i.e., Jasper National Park; 2,303-km^2) authority and characterized by recreational use. Mountainous land cover

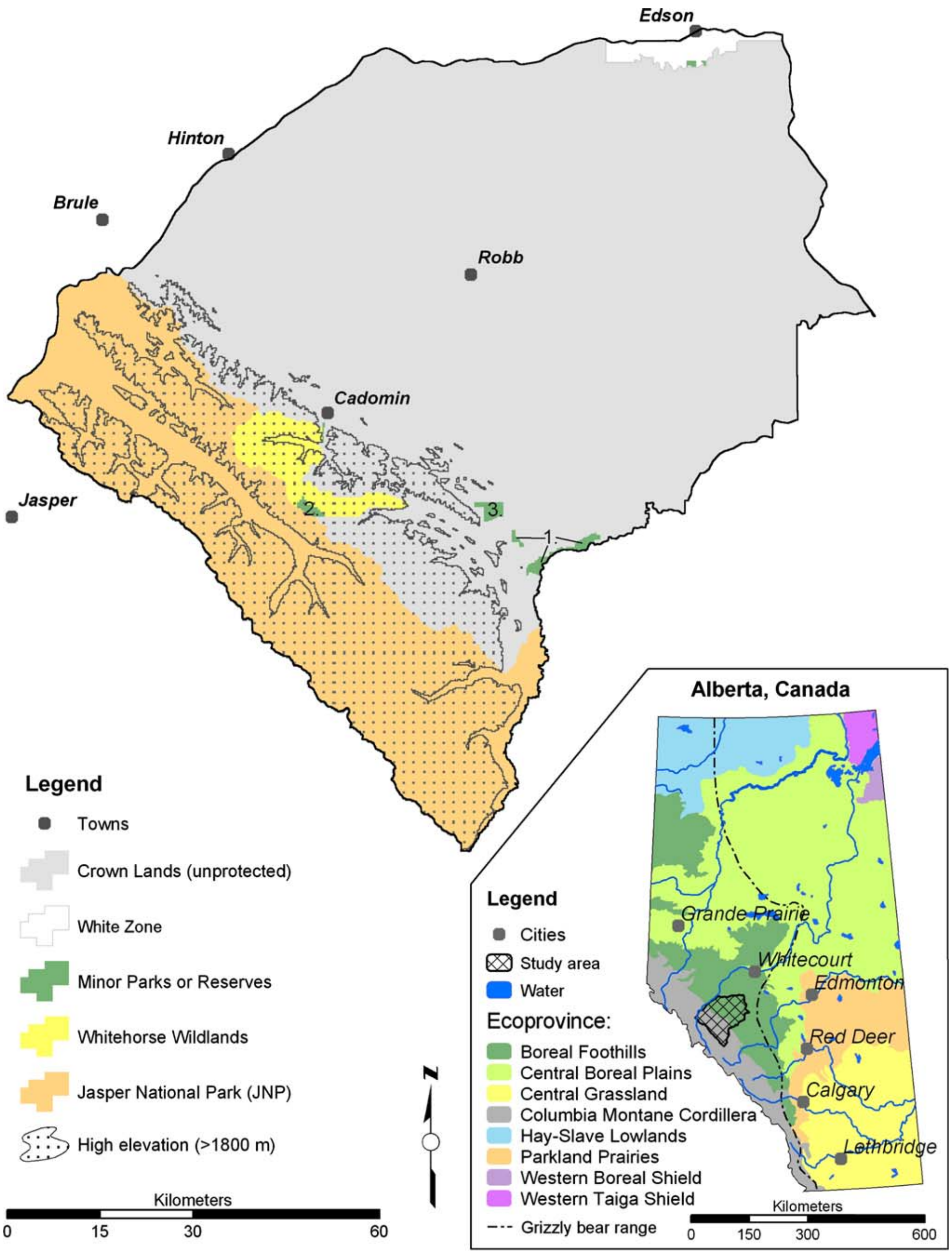

Fig. 1 – Study area map depicting management zones, towns, and high elevation (>1800 m) sites. Minor parks or reserves mentioned include: (1) Brazeau Canyon; (2) Cardinal Divide; (3) Grave Flats. Inset map of Alberta in lower right illustrates Ecoprovince, grizzly bear range, and study area within Alberta.

classes consisted of montane forests, conifer forests, sub-alpine forests, alpine meadows, and high elevation areas of rock, snow, and ice (Achuff, 1994; Franklin et al., 2001). Foothills, on the other hand, were characterized by a number of resource extraction activities, including forestry, oil and gas, and open-pit coal mining. Large numbers of roads and seismic lines typify this landscape. Land cover for the foothills includes conifer, mixed, and deciduous forests, areas of open and treed-bogs, small herbaceous meadows, and areas of regenerating (fire and clearcut harvesting) forests (Achuff, 1994; Franklin et al., 2001). With a short growing season, lack of salmon and other high protein foods (Jacoby et al., 1999), this interior population of grizzly bears occurs at low densities (e.g., <14 animals/1000-km^2).

3. Methods (a framework for assessing grizzly bear habitat)

3.1. *Modelling the relative probability of adult female occupancy*

We used a resource selection model specific to adult females during late hyperphagia from Nielsen (2005) to define the relative probability of adult female occurrence. We chose a single sex-age group, as Nielsen (2005) found differences in habitat selection between sub-adult, adult male and adult female grizzly bears. As adult female grizzly bears represented the most sensitive sex-age class for population change (Knight and Eberhardt, 1985; Wiegand et al., 1998; Boyce et al., 2001), we chose to map adult female habitat. As seasonal variation in habitat use is common (Hamer and Herrero, 1987; Hamer et al., 1991; Nielsen et al., 2002, 2003; Nielsen, 2005), we chose to map late hyperphagia, defined to be 16 August to 15 October. Late summer and fall is largely considered the most critical foraging period for grizzly bears, corresponding to the ripening of fruit from *Vaccinium* spp. and *Shepherdia canadensis* (Hamer and Herrero, 1987; Hamer et al., 1991; Nielsen et al., 2004c).

Using 5172 late hyperphagia radiotelemetry observations collected from 13 adult females between 1999 and 2002, we developed a habitat model predicting the relative probability of adult female occurrence (Nielsen, 2005). The model was assumed to take an exponential form (Manly et al., 2002):

$$H_f = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_{24} x_{24}), \tag{1}$$

where H_f represented the relative probability of occurrence for adult females within any study area pixel (30 m × 30 m), and the βs the selection coefficients for 24 categorical and continuous environmental predictor variables used to describe adult female grizzly bear habitat for the late summer and fall period (Tables 1 and 2). Variables included 10 land cover categories, distance to nearest edge, a terrain-derived index of soil wetness, an index of terrain ruggedness, forest or regenerating forest age, global solar radiation within 3 land cover types (interactions), and the interactions of soil wetness with either edge distance or forest age. Map predictions were binned into 10 ordinal habitat classes, ranging from a low relative probability of occurrence for bin 1 to a high relative probability of occurrence for bin 10 (Fig. 2a). Based on average bin values within land cover classes, adult females favored alpine/herbaceous, open conifer, and deciduous forests, while tending to avoid anthropogenic, regenerating forests, and non-vegetated areas. General distribution corresponded to mid-to-high elevation sites in the mountains, throughout the Gregg and upper McLeod River basins, and in the foothills near the town of Robb (Fig. 2a). Evaluations of the map performance using 1201 independent radiotelemetry observations collected from 7 adult females during 2003 revealed a significant predictive fit (Nielsen, 2005).

3.2. *Modelling risk of human-caused grizzly bear mortality*

We used a model from Nielsen et al. (2004a) to define risk of human-caused mortality for adult grizzly bears. The risk model, developed just south of the study area, described the distribution of grizzly bear mortalities based on a comparison of human-caused grizzly bear mortalities with random landscape locations using common landscape covariates that represented human encroachment and bear habitat. Risk of human-caused mortality for adult female grizzly bears, R_f, was fit for the present study area using coefficients reported for adult bears from Nielsen et al. (2004a) and defined as

$$R_f = \exp(0.42d + 0.50g + 0.59n + 1.02s - 0.15r - 11.74z - 1.49w - 2.90a - 6.74t). \tag{2}$$

Environmental covariates included, deciduous forest (d), grassland and crop (g), non-vegetated areas (n), and shrub (s) land cover categories (coded as 0 or 1); greenness (r), an index of vegetative productivity based on a tasseled-cap transformation of Landsat TM bands; distance to nearest edge (z), water (w) or human access (a) feature measured in kilometers; and terrain ruggedness (t). Resulting predictions of human-caused mortality risk (R_f) were highest when near edges, water, and

Table 1 – Remote sensing and GIS environmental predictor variables used for modelling the relative probability of occurrence for adult female grizzly bears during late hyperphagia in west-central Alberta, Canada

Model variable	Variable code	Linear or non-linear	Units/scale	Data range
Land cover				
Alpine/herbaceous	Alpine	Category	n.a.	0 or 1
Anthropogenic	Anthro	Category	n.a.	0 or 1
Closed conifer	Clscon	Category	n.a.	0 or 1
Deciduous forest	Decid	Category	n.a.	0 or 1
Mixed forest	Mixed	Category	n.a.	0 or 1
Non-vegetated	Nonveg	Category	n.a.	0 or 1
Open-bog/shrub	Opnbog	Category	n.a.	0 or 1
Open conifer	Opncon	Category	n.a.	0 or 1
Regenerating forest	Regen	Category	n.a.	0 or 1
Treed-bog	treedbg	Category	n.a.	0 or 1
Edge distance	Edge	Linear	100 m	0–35
Compound topographic index	Cti	Non-linear	Unitless	1.89–31.7
Terrain ruggedness index	Tri	Non-linear	Unitless	0–0.29
Forest age	For-age	Non-linear	10-year-age class	1–15
Regenerating clearcut age	Cut-age	Non-linear	10-year-age class	1–5
Solar radiation × alpine	Solar × alp	Linear	kJ/m^2	17,133–91,836
Solar radiation × clscon	Solar × clscon	Linear	kJ/m^2	21,698–91,835
Solar radiation × regen	Solar × regen	Linear	kJ/m^2	57,110–91,831
Cti × age	Cti × age	Linear	Unitless	0–402
Cti × edge distance	Cti × edge	Linear	Unitless	0–522

Table 2 – Estimated habitat selection coefficients for adult female grizzly bears in west-central Alberta, Canada based estimates from Nielsen (2005)

Environmental variable	Coefficient	SE	p
Alpine/herbaceous	0.218	0.941	0.817
Anthropogenic	−0.114	0.344	0.740
Closed conifer forest	2.530	0.703	<0.001
Deciduous forest	1.366	0.309	<0.001
Mixed forest	0.778	0.553	0.159
Non-vegetated	0.510	0.445	0.252
Open-bog/shrub	0.322	0.502	0.522
Open conifer forest	1.909	0.348	<0.001
Regenerating forest	−8.865	2.856	0.002
Treed-bog	1.346	0.377	<0.001
Edge distance	−0.302	0.061	<0.001
Cti	0.107	0.049	0.029
Cti^{2a}	−0.294	0.195	0.130
Tri	34.009	7.564	<0.001
Tri^{2}	−147.07	31.84	<0.001
For-age	−0.219	0.058	<0.001
For-age^{2a}	0.766	0.364	0.036
Cut-age	−0.262	0.390	0.545
Cut-age^{2}	0.097	0.075	0.197
$\text{Solar} \times \text{clscn}^{b}$	−0.207	0.093	0.026
$\text{Solar} \times \text{regen}^{b}$	0.934	0.355	0.009
$\text{Solar} \times \text{alp}^{b}$	0.166	0.123	0.180
$\text{Cti} \times \text{age}^{a}$	0.633	0.126	<0.001
Cti × edge	0.017	0.005	<0.001

Robust standard errors and significance levels (p) were estimated from modified sandwich estimates of variance among animals with categorical contrasts from deviance coding.

a Estimated coefficients and standard errors reported at 100 times their actual value.

b Estimated coefficients and standard errors reported at 10,000 times their actual value.

access, as well as in areas with lower greenness values and in shrub habitats (Nielsen et al., 2004a). Using Eq. (2), we calculated R_f for the given study area. Predicted values of R_f were scaled in a similar manner to that of H_f (10 ordinal bins using a quantile method), where the relative risk of mortality ranged from a low of 1 to a high of 10 (Fig. 2b). Assessment of mortality locations occurring within the defined study suggested good accuracy to the R_f model with 10 of 13 (6 of 6 for female bears) documented human-caused grizzly bear mortalities with accurate coordinates occurring in R_f bins greater than five.

3.3. *Defining attractive sink and safe harbour indices*

Using the adult female habitat occupancy (H_f) and a mortality risk (R_f) maps, we defined a two-dimensional habitat model combining relative probability of occurrence with relative risk of mortality. For conservation purposes, we were particularly interested in identifying 2 habitat conditions, attractive sink habitats (Delibes et al., 2001; Naves et al., 2003), also known as ecological traps (Dwernychuk and Boag, 1972; Ratti and Reese, 1988; Donovan and Thompson, 2001); and the corollary safe-harbour sites (source-like areas). Attractive sink and safe-harbour indices were assumed to correlate with mortality risk and reproduction, respectively. We defined attractive sink and safe harbour indices as

$$\mathrm{AS_f} = \mathrm{H_f} \times \mathrm{R_f} \tag{3}$$

and

$$\mathrm{SH_f} = \mathrm{H_f} \times (11 - \mathrm{R_f}), \tag{4}$$

where $\mathrm{AS_f}$ and $\mathrm{SH_f}$ were indices of attractive sink and safe harbour habitats for adult females, respectively, H_f an index of habitat occupancy for adult females from Eq. (1), and R_f an index of human-caused mortality risk for adult animals

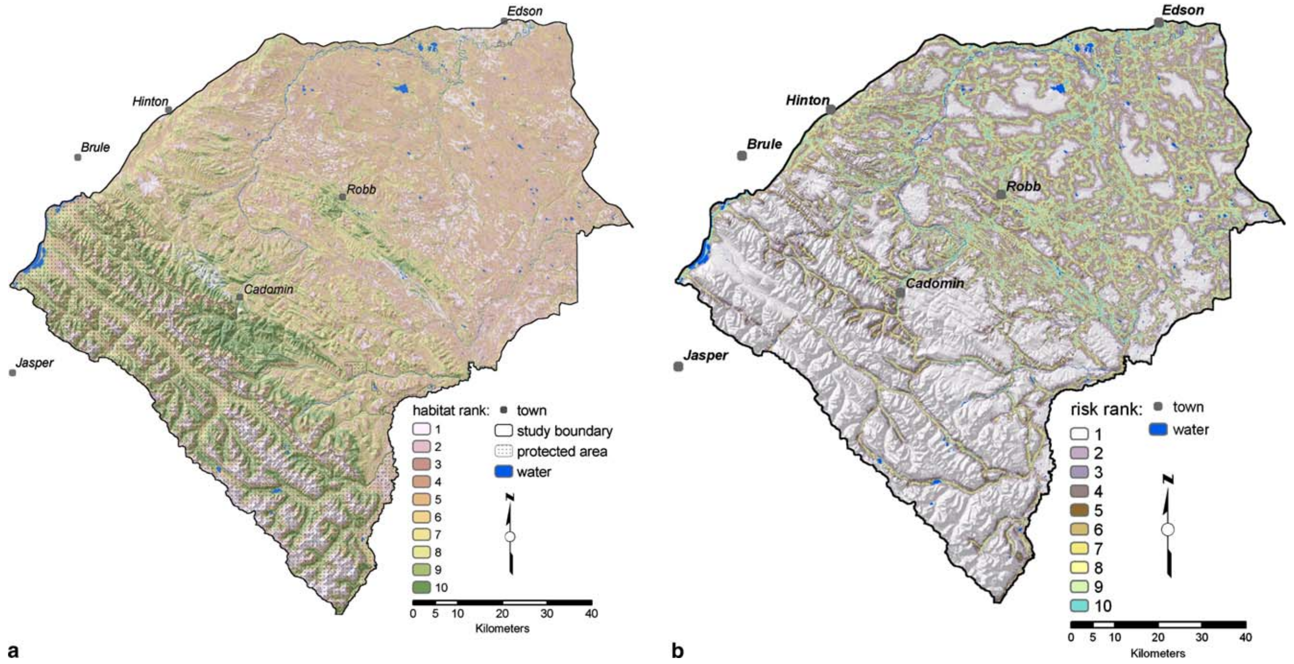

Fig. 2 – Predicted relative probability of occurrence in ordinal bins (1-low to 10-high) for adult female grizzly bears during late hyperphagia (16 August to 15 October) (a). Risk of human-caused mortality in ordinal bins (1-low to 10-high) for adult female grizzly bears in west-central Alberta, Canada (b).

from Eq. (2). As H_f was assumed to be proportional to the relative probability of use, when multiplied by the relative probability of mortality risk (R_f), an index of both occupancy and mortality risk resulted. Given that both H_f and R_f scaled from 1 to 10, AS_f and SH_f indices ranged from a possible low value of 1 to a high value of 100 (Fig. 3a and b). High AS_f values were taken to represent habitats in which bears were both likely to occur and at risk of human-caused mortality (e.g., low survival), whereas high SH_f values were assumed to indicate habitats in which bears were likely to occur, but also low in risk of mortality. To understand the distribution of SH_f and AS_f sites, we assessed the proportion of the landscape within AS_f or SH_f conditions based on very low (1–20), low (21–40), mid (41–60), high (61–80), and very high (81–100) AS_f or SH_f values (Fig. 3a and b). We summarized AS_f and SH_f pixels by management authority, as well as characterizing (mean and standard deviation) each index within individual land cover categories to better understand spatial patterns of the two indices, while further suggesting where protection and mitigation are needed.

3.4. *Defining habitat states*

As well as defining safe-harbour and attractive-sink indices, we also suggest a model of 5 relative habitat states based on the two-dimensional habitat model. We defined the 5 habitat states to be non-critical habitat, primary sink, secondary sink, primary habitat, and secondary habitat, based on the division of H_f into 3 categories and R_f into 2 classes (Fig. 3c). Although producing 6 possible states, 2 states were merged into a single habitat state called non-critical habitat and defined as $H_f < 5$, regardless of R_f. Non-critical habitats were not considered to be matrix habitats where female bear occupancy never occurred, but rather where we expected them to be rare. Secondary habitats were defined where H_f values were between 5 and 7 and $R_f < 6$ (e.g., low risk and moderate habitat occupancy). Primary habitats, on the other hand, were defined as those sites with $H_f > 7$ and $R_f < 6$ (e.g., low risk and high habitat occupancy). Secondary sinks were defined as those sites with H_f between 5 and 7 and $R_f > 5$ (e.g., high risk and moderate habitat occupancy). Lastly, primary sinks were defined to be those sites with $H_f > 7$ and $R_f < 6$ (e.g., low risk and high habitat occupancy). Primary sinks would correspond to high attractive-sink values, while primary habitats would be most similar to high values of safe-harbour. Habitat states by management authority were summarized, as well as descriptions of each state within individual land cover categories to better understand the distribution of defined habitat states and sites needing protection or mitigation.

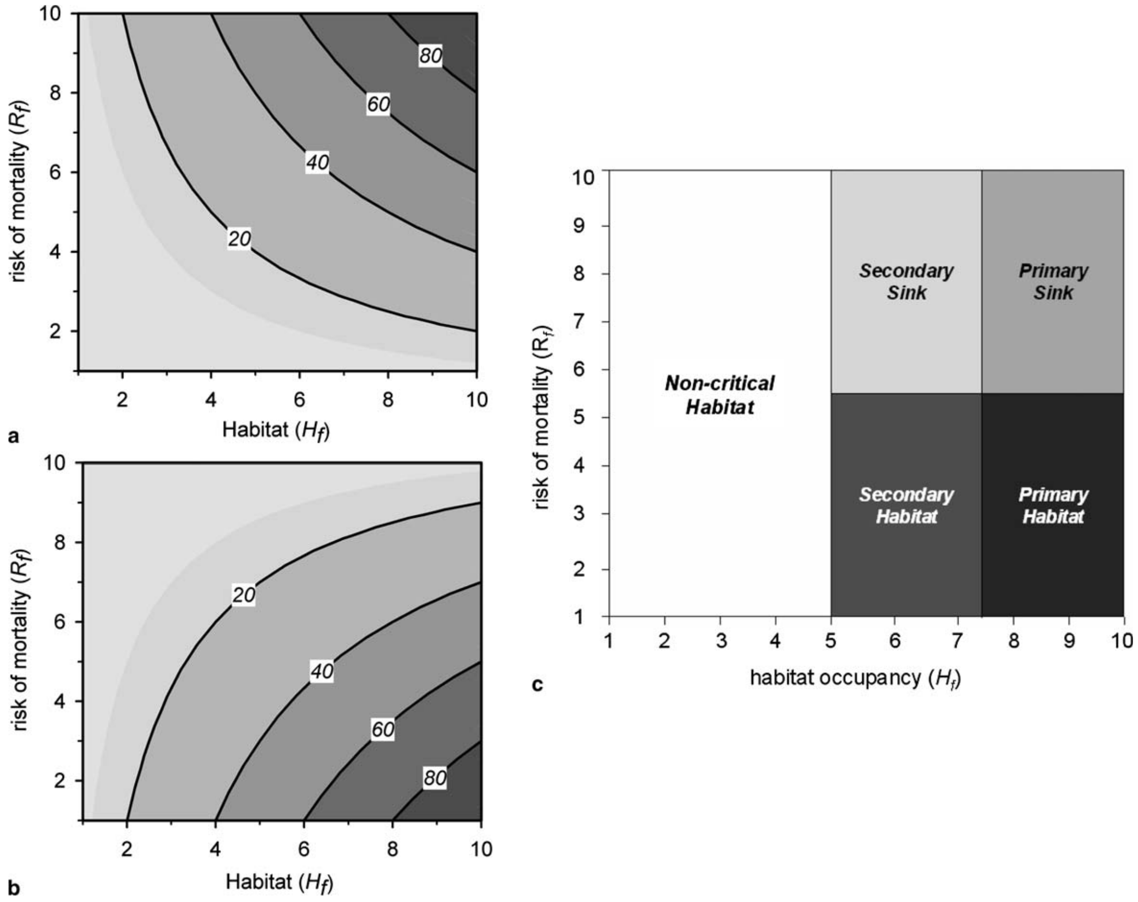

Fig. 3 – Graphic representation of attractive sink (AS_f) index (a), safe harbour (SH_f) index (b), and 5 habitat states (c) based on adult female habitat (H_f) and human-caused mortality risk (R_f) models. Categories for AS_f and SH_f indices were defined as very low (1–20), low (20–40), mid (40–60), high (60–80), and very high (80–100).

4. Results

4.1. *Index of attractive-sink habitat*

The majority (67.8%) of the area was dominated by very low attractive sink (AS_f) values with decreasing amounts of low (17.6%), mid (9.1%), high (4.2%), and very high (1.3%) categories (Fig. 4a). Although high and very high AS_f categories totaled just over 5% of the landscape, they were concentrated to the foothills near Robb, many of the upper foothill river valleys, and mountain passes and drainage networks in Whitehorse Wildlands and adjacent Jasper National Park (Fig. 4a). In the foothills, most attractive sink locations were the result of increased access due to forestry and oil and gas activities. Average attractive sink values for the 5 examined protected areas, the white zone and crown lands revealed low to very low overall ratings (Table 3). Attractive sink values for Jasper National Park (JNP), however, were nearly half those of Brazeau Canyon, Cardinal Divide, Grave Flats, Whitehorse Wildlands, the white zone, and crown lands.

Values of the AS_f index varied among land cover classes (Table 3). Non-vegetated and deciduous forests had the lowest and highest AS_f values, respectively, ranging from very low to moderate values. Although regenerating forests and closed conifer forests were not as low as non-vegetated areas, they too averaged very low AS_f values. Only the deciduous forest class was classified with a mid AS_f level, although both anthropogenic and open-bog/shrub classes nearly approached deciduous forest values having an average AS_f near 30. Alpine/herbaceous, mixed forests, open conifer forest, and treed-bog habitats were all similar in composition, having low AS_f scores ranging from 25 to 27.8 (Table 3).

4.2. *Index of safe-harbour habitat*

Very low safe-harbour (SH_f) scores dominated (34.9%) the study region (Fig. 4b). Unlike that of the AS_f index, more balanced levels of low (23.8%), mid (16.8%), high (13.7%), and very high (10.9%) SH_f categories were evident. High and very high safe harbour values were most common to intermediate elevations within mountain valleys and along the Front Range (Fig. 4b). Some of the lower foothills near Robb also contained high safe harbour levels, but were much more limited in amount and isolated in nature. Examinations of SH_f values within protected and non-protected areas revealed greater differentiation of SH_f values than AS_f values, varying from high to very low values (Table 3). Cardinal Divide and the white zone had very low SH_f values, while Whitehorse Wildlands had high SH_f values. Brazeau Canyon, Grave Flats and JNP all averaged moderate SH_f values, while the crown lands averaged low SH_f values.

Safe-harbour values varied substantially among land cover classes from very low to very high levels (Table 3). Alpine/herbaceous, followed closely by open conifer forest had very high and high SH_f values, respectively, while as would be expected the anthropogenic class was very low in SH_f values. Regenerating forest, open-bog/shrub and mixed forest also had low SH_f values (Table 3). Intermediate (mid-SH_f values) between alpine/herbaceous and anthropogenic classes was closed conifer and deciduous forests, non-vegetated areas and treed-bog habitats.

4.3. *Two-dimensional habitat states*

For the given study area and defined habitat states, we predicted 39.6% of the study area to be non-critical, 9.8% to be

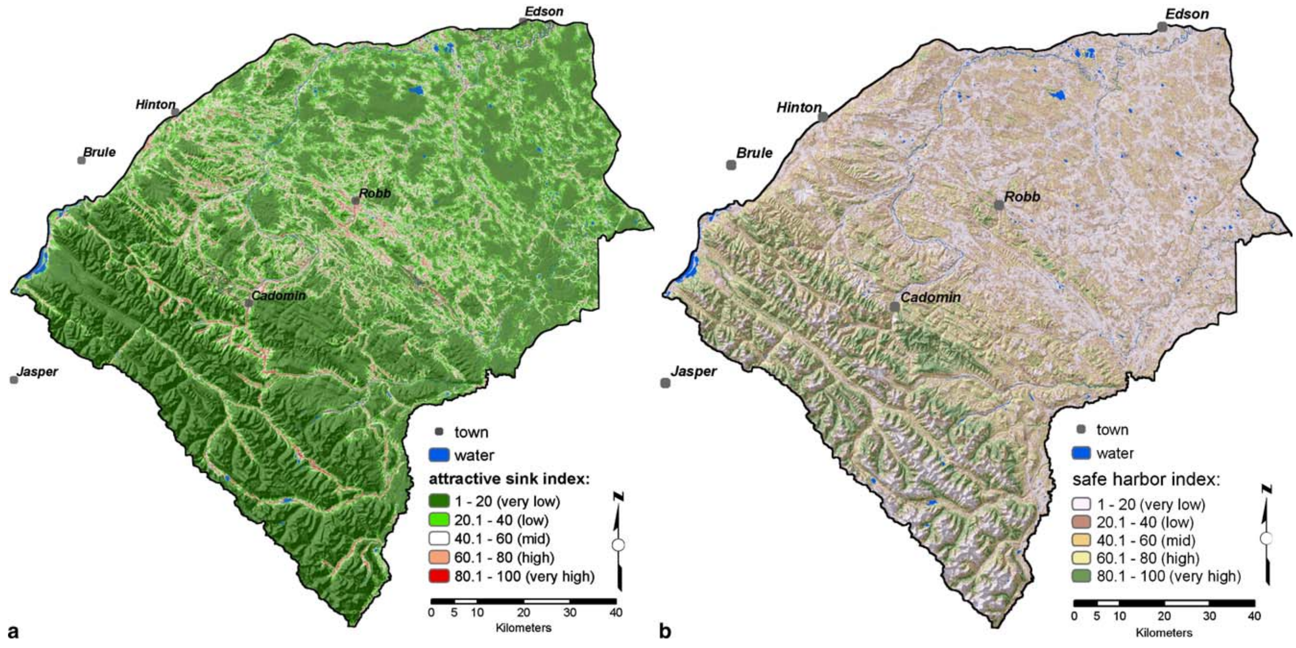

Fig. 4 – Index of attractive sink (AS_f) habitats (a) and safe harbour (SH_f) habitats (b) for adult female grizzly bears during late hyperphagia. High to very high attractive sink values represent those habitats where animals are both likely to occur and at high risk of mortality (i.e., mitigation sites), while high to very high safe harbour values represent those habitats where animals are likely to occur and are at low risk of mortality (i.e., targets for protection).

Table 3 – Characteristics (mean, standard deviation [SD], and category) of attractive sink (AS_f) and safe harbour (SH_f) indices for management zones and land cover classes

Management zone or land cover type	Attractive sink (AS_f)			Safe harbour (SH_f)		
	Mean	SD	Category	Mean	SD	Category
(a) Management zone						
Brazeau Canyon (Wildland Park)	23.8	18.9	Low	42.9	23.4	Mid
Cardinal Divide (Natural Area)	22.9	30.9	Low	19.4	17.7	Very low
Grave Flats (Natural Area)	29.3	24.1	Low	41.2	20.9	Mid
Jasper (National Park)	12.5	17	Very low	53.8	32	Mid
Whitehorse (Wildland Park)	21.2	21.6	Low	64.5	28.2	High
White-zone (Private)	24.6	21.4	Low	15.5	16.8	Very low
Crown lands	21.6	20.0	Low	35.8	25.4	Low
(b) Land cover class						
Alpine/herbaceous	25	25.3	Low	80.2	29.1	Very high
Anthropogenic	38.4	22.5	Low	10.5	11.4	Very low
Closed conifer forest	14.2	13.9	Very low	42.2	24.7	Mid
Deciduous forest	40.5	28.9	Mid	50.3	25.6	Mid
Mixed forest	26.7	19.8	Low	32.1	20.3	Low
Non-vegetated	10.8	17	Very low	42.7	30.9	Mid
Open-bog/shrub	32.5	20.1	Low	24.5	17.2	Low
Open conifer forest	27.8	23.9	Low	79.9	24.5	High
Regenerating forest	14	14.9	Very low	21.5	21.9	Low
Treed-bog	25.7	18.9	Low	44.2	18.5	Mid

secondary sink, 6.7% to be primary sink, 22.0% to be secondary habitat, and 21.9% to be primary habitats (Fig. 5a). These percentages varied by land cover with the highest proportion of primary habitats occurring in open conifer (81.1%) and alpine/herbaceous (80.7%) classes and the lowest amounts of primary habitat in open-bog/shrub (2.6%) and anthropogenic (1.3%) classes (Table 4). Secondary habitat conditions were common for treed-bog (48.3%) and non-vegetated (48.3%) classes, while secondary habitats were rare for the high valued alpine/herbaceous (0.6%) or open conifer (0.7%) classes. Primary sink habitats were most prominent for deciduous forests (32.3%) and to a lesser degree open conifer (18.0%) and alpine/herbaceous (15.4%) classes. Closed conifer and regenerating forests had low amounts of primary sink habitats (Table 4). Both classes, however, were low in habitat quality as supported by the classification of non-critical habitats,

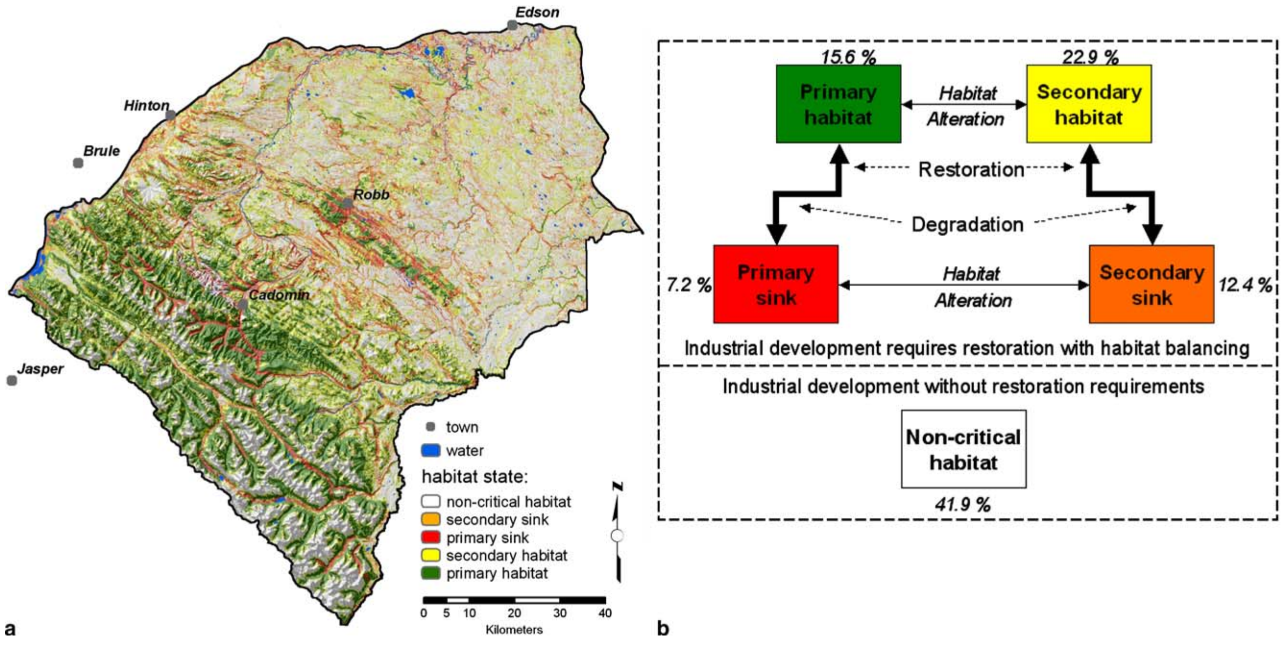

Fig. 5 – Predicted habitat states for west-central Alberta based on a two-dimensional classification of habitat occupancy (H_f) and mortality risk (R_f) predictions (a). Schematic representation of accounting of habitat states on crown lands of west-central Alberta with percentages for each state provided (b). Using a no net loss strategy, balancing of habitat states would be required.

Table 4 – Percent composition of 5 hypothetical habitat categories for management zones (a) and land cover classes (b)

Management or land cover	Non-critical habitat	Secondary sink	Primary sink	Secondary habitat	Primary habitat
(a) Management zone					
Brazeau Canyon (Wildland Park)	29.2	10.2	4.8	32	23.9
Cardinal Divide (Natural Area)	61.7	6.7	17.4	8.4	5.7
Grave Flats (Natural Area)	19.2	12.6	15.4	36.2	16.6
Jasper (National Park)	33.6	2.2	4.6	20	39.6
Whitehorse (Wildland Park)	16.0	0.9	10.9	14.5	57.6
White zone (Private)	63.2	14.8	9.7	8.0	4.2
Crown lands	41.9	12.4	7.2	22.9	15.6
(b) Land cover class					
Alpine/herbaceous	3.2	0.1	15.4	0.6	80.7
Anthropogenic	57.9	24.3	14.6	1.9	1.3
Closed conifer forest	44.7	5.2	2.9	27.5	19.7
Deciduous forest	0.7	11.3	32.3	14.7	41
Mixed forest	38.8	19.5	8.7	23.2	9.9
Non-vegetated	9.2	16.9	10.3	48.3	15.4
Open-bog/shrub	34.6	35.7	5.5	21.7	2.6
Open conifer forest	0	0.2	18	0.7	81.1
Regenerating forest	72.6	5.2	2.7	11.9	7.7
Treed-bog	9.2	16.9	10.3	48.3	15.4

with the majority of regenerating forests (72.6%), anthropogenic (57.9%) and closed conifer (44.7%) sites considered non-critical. Finally, secondary sinks were most common for open-bog/shrub (35.7%) and anthropogenic (24.3%) classes, while least frequent for alpine/herbaceous (0.1%) and open conifer forest (0.2%) sites (Table 4).

Within the protected and non-protected management zones, Whitehorse Wildlands had the highest proportion of primary habitats and the lowest proportion of non-critical habitats and secondary sinks (Table 4). Although having a larger proportion of primary habitats, Whitehorse Wildlands did have a low, but noticeable composition of primary sinks along recreational trails. In contrast to Whitehorse Wildlands, JNP had moderate proportions of primary and non-critical habitats, reflecting the distinction between high elevation rocky peaks and glaciers that were poor in habitat quality and high-quality alpine meadows (Table 4). Although JNP was moderate in total habitat value, both primary and secondary sinks were rather rare overall, indicating a high level of security from human-caused mortality. The Cardinal Divide, being adjacent to JNP and Whitehorse Wildlands, had the greatest proportion of non-critical habitats and the lowest proportions of primary and secondary habitats for examined protected areas (Table 4). As well, primary sinks were more dominant at the Cardinal Divide reserve than all other management zones. This suggested that what little habitat was available for bears at the Cardinal Divide site were non-secure in nature. Grave Flats and Brazeau Canyon both contained moderate proportions of secondary habitats with lesser amounts of primary habitats. However, unlike that of Grave Flats, Brazeau Canyon had higher proportions of non-critical habitats and lower proportions of primary sinks (Table 4). Finally, the white zone and crown lands showed high proportions of non-critical habitat, although crown lands did contain moderate amounts of secondary and primary habitats unlike that of the white zone that contained very little secondary or primary habitat.

5. Discussion

5.1. *A conservation strategy using habitat indices*

The index of attractive-sink habitat was on average rather low for examined management zones and land cover classes in west-central Alberta. Selected areas, however, had concentrated high and very high categories of attractive sink, indicating a co-occurrence of high mortality risk and animal occupancy. This was most apparent for forest edges associated with forestry activities and roads associated with both forestry and oil and gas operations. Significant numbers of grizzly bear mortalities can result in these rare, yet concentrated sites (Nielsen et al., 2004a). For the Banff and Yoho National Parks (within the CRE), where portions of high and very high risk were even lower, Benn and Herrero (2002) documented an average annual human-caused mortality of 4.3 bears/year for the period 1971 to 1998. For a protected (national park) population that lacked hunting and industrial resource pressures, these mortalities combined with natural causes of death can be a significant conservation concern. Including Provincial lands where hunting and resource extraction occurred, average annual mortality was higher at 7.6 bears/year, representing an estimated mortality rate of 6.1–8.3% of the population and exceeding the Provincial allowable threshold of 6% (Benn, 1998). Even isolated but concentrated levels of attractive sink can lead to mortality sinks (*sensu* Knight et al., 1988). Limiting human access and/or modifying habitat quality to make areas where bears are likely to encounter humans less attractive or accessible to bears or humans should be considered, especially those attractive sinks that occur near contiguous areas of safe harbour habitats. Although not as evident during late hyperphagia, grizzly bears also readily used clearcuts in the foothills during pre-berry seasons (Nielsen et al., 2004b). As we considered only late hyperphagia, identification of attractive sinks at clearcut sites during earlier seasons also should be considered.

Unlike the attractive-sink index, the index of safe-harbour habitats identified existing high-quality and secure grizzly bear habitats. Maps of safe-harbour habitats differed from traditional radiotelemetry-based maps of grizzly bear occurrence in Alberta (e.g., Nielsen et al., 2002, 2003; Theberge, 2002), because they also consider security (low mortality risk), similar to concepts of habitat effectiveness and security (i.e., Gibeau, 1998; Gibeau et al., 2001). For west-central Alberta, safe-harbour values averaged from very low to very high depending on land cover class and management zone. Generally, high-valued safe-harbour habitats were most common to the front slopes of the Rocky Mountains, along with isolated foothill ranges in the east (especially near the town of Robb), and interior valleys or side slopes in Jasper National Park. Overall, the protected Whitehorse Wildlands averaged the highest safe-harbour values for management zones, indicating the significance of this park for grizzly bear conservation. Alpine/herbaceous and open conifer stands also proved high to very high in average safe-harbour values, consistent with previous regional habitat assessments promoting secure open herbaceous areas and open forested conditions (Hamer and Herrero, 1987; Hamer et al., 1991; McLellan and Hovey, 2001; Nielsen et al., 2002, 2003; Theberge, 2002).

Selective harvesting of mature forest stands during winter with immediate removal (decommission) of temporary winter forest roads provides one approach for improving habitat quality and limiting human-caused mortality risk. Care should be given towards the silvicultural practice employed for site preparation and shape of harvest blocks, as grizzly bears have been shown to select clearcuts based on method of scarification and shape of clearcut (Nielsen et al., 2004b). Irregular-shaped clearcuts proved more attractive to bears (Nielsen et al., 2004b), while silvicultural practices can influence food resource availability (Nielsen et al., 2004c). As forests and regenerating clearcuts age, attractive sink and safe harbour values change, even without changes in the human footprint. Given the dynamic nature of grizzly bear habitats, future scenario modelling should be used to consider long-term impacts of resource management practices. We consider the identification of attractive sink and safe harbour sites as an essential element of grizzly bear management. Indices of attractive sink provide a mechanism for identifying areas in most need of management attention to minimize the likelihood of contact between humans and bears, while safe-harbour sites identify habitats in most need of continual protection or inclusion in a system of reserves.

5.2. *A conservation strategy using habitat states*

Instead of using attractive sink and safe-harbour indices, which were continuous metrics of non-secure and secure habitat, we proposed an approach that identified categorical states based once again on the two-dimensional model of habitat occupancy and mortality risk (similar to Naves et al., 2003). Using thresholds of mortality risk (2 categories) and habitat occupancy (3 categories), we defined non-critical habitats, secondary and primary sinks, and secondary and primary habitats. Primary habitats closely corresponded to high safe-harbour scores, while primary sinks were associated with high attractive sink values. Proportions of each habitat state varied among management zone and land cover class with overall composition dominated by non-critical habitat, followed by secondary habitat, primary habitat, secondary sink, and primary sink. Although primary sinks were low in overall composition, they were concentrated to river bottoms and valleys. For some regions within the Whitehorse Wildlands and Jasper National Park, sink habitats were potentially over-predicted. Recreational use was lower in these Parks than Banff National Park to the south where the baseline mortality model was estimated (Nielsen et al., 2004a). Replacing primary and secondary sinks with primary and secondary habitats for low use recreational trails in Jasper and Whitehorse Wildlands should be considered. Regardless, patterns of primary and secondary sinks and habitats within crown lands, where the majority of human activities and conservation concerns reside, appear reasonable.

We propose that stakeholders involved in grizzly bear management and conservation on Alberta crown lands consider tracing changes within the 5 hypothetical habitat states during resource planning. Specifically, we suggest a goal of no net loss for secondary and especially primary habitats. If resource management actions modify secondary or primary habitats to secondary or primary sinks through increases in human access, equivalent amounts of secondary or primary sinks should be restored through management of human access (see Fig. 5b). Seasonal variation in habitat use caused by changes in availability of critical foods (Nielsen et al., 2003) should also be considered. Most generally, however, the late summer and fall period examined here is largely regarded as the most important season for acquiring calories and the riskiest for survival (Benn, 1998; Benn and Herrero, 2002).

Future scenario modelling of grizzly bear habitat states should be considered for all long-term forest management plans occurring in grizzly bear range. Using such methods, Nielsen (2005) demonstrated potential changes in attractive sink, safe harbour, and habitat states over a 100 period. By using optimization modelling, both grizzly bear habitat and timber or other natural resources could be co-managed for sustainability. On-the-ground restoration of sink habitat or preservation of source habitat should consider landscape configuration, so that activities are best situated to habitats most accessible to bears. A moving window analysis of habitats at the size of female home ranges or larger (Nams et al., 2006) could be used to define landscape configuration of habitat. For reserve planning, we suggest that primary and secondary habitats be used, since these sites represent remaining secure habitats. Necessarily, such reserves would need to encompass multiple territory units. Road development within such reserves should be limited or requiring strict human access control, restoration of similar habitats elsewhere and finally deactivation and re-vegetation of roads following final extraction of resources.

6. Conclusions and management recommendations

Grizzly bear habitat modelling rarely considers spatial predictions of survival, the most important life history trait for bears, focusing on occupancy patterns instead. As survival can vary among different habitats and human-related landscape patterns (Naves et al., 2003; Nielsen et al., 2004a; Johnson et al., 2004), relying on animal occurrence alone for assessments of habitat quality is questionable. One risks promoting habitats that are effectively attractive sinks where occupancy and reproduction may be high, but survival is low (Delibes et al., 2001). In Alberta, grizzly bears are being considered for threatened status within the Province (Stenhouse et al., 2003). Managers therefore require tools for inventorying grizzly bear habitats, identifying key sites for protection, and finally identifying those areas in greatest need of management attention. Using a two-dimensional habitat model of occupancy and mortality risk, we developed habitat indices and habitat states for the purpose of better identifying these grizzly bear conservation needs. Indices of attractive sink, the corollary safe-harbour habitats, and habitat states were calculated from the 2 dimensions to describe patterns of non-secure and secure high-quality habitats. We recommend that stakeholders involved in resource management of Alberta's foothills consider our two-dimensional habitat models for grizzly bear conservation planning. To minimize risk of decline in grizzly bears, we suggest that when industrial resource extraction modifies an existing primary or secondary habitat, restoration of equivalent primary or secondary sinks in other sites should be considered (i.e., no net loss). Non-critical habitats, on the other hand, could be managed without strict mitigation. Landscape patterns should be considered when targeting restoration sites to avoid isolation of sites within a matrix of risky habitat. Managing human behaviour to reduce habituation of bears and development of problem bears, a major source of human-caused mortality (Benn, 1998; Benn and Herrero, 2002), should be a priority. An effective education program provides an important mechanism for successfully reducing bear-human conflict (Schirokauer and Boyd, 1998). Finally, future scenario modelling should be employed to understand long-term impacts of resource development and forest succession on grizzly bear habitat needs (Nielsen, 2005).

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REFERENCES

Achuff, P.L., 1994. Natural Regions, Sub-regions and Natural History Themes of Alberta; A Classification for Protected Areas Management. Alberta Environmental Protection, Edmonton, Alta., Canada.

Apps, C.D., McLellan, B.N., Woods, J.G., Proctor, M.F., 2004. Estimating grizzly bear distribution and abundance relative to habitat and human influence. Journal of Wildlife Management 68, 138–152.

Benn, B., 1998. Grizzly bear mortality in the Central Rockies Ecosystem, Canada. M.Sc. Thesis, University of Calgary, Calgary, Alta., Canada.

Benn, B., Herrero, S., 2002. Grizzly bear mortality and human access in Banff and Yoho National Parks, 1971–1998. Ursus 13, 213–221.

Boyce, M.S., McDonald, L.L., 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14, 268–272.

Boyce, M.S., Blanchard, B.M., Knight, R.R., Servheen, C., 2001. Population viability for grizzly bears: a critical review. International Association of Bear Research and Management, Monograph Series Number 4, p. 39.

Boyce, M.S., Waller, J.S., 2003. Grizzly bears for the Bitterroot: predicting potential abundance and distribution. Wildlife Society Bulletin 31, 670–683.

Breininger, D.R., Carter, G.M., 2003. Territory quality transitions and source-sink dynamics in a Florida Scrub-Jay population. Ecological Applications 13, 516–529.

Delibes, M., Gaona, P., Ferreras, P., 2001. Effects of an attractive sink leading into maladaptive habitat selection. American Naturalist 158, 277–285.

Dobson, A.B., Rodriguez, J.P., Roberts, W.M., Wilcove, D.S., 1996. Geographic distribution of endangered species in the United States. Science 275, 550–553.

Donovan, T.M., Thompson, F.R., 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. Ecological Applications 11, 871–882.

Dwernychuk, L.W., Boag, D.A., 1972. Ducks nesting in association with gulls-ecological trap. Canadian Journal of Zoology 50, 559–563.

Flather, C.H., Knowles, M.S., Kendall, I.A., 1998. Threatened and endangered species geography. Bioscience 48, 365–376.

Franklin, A.B., Anderson, D.R., Gutiérrez, R.J., Burnham, K.P., 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70, 539–590.

Franklin, S.E., Stenhouse, G.B., Hansen, M.J., Popplewell, C.C., Dechka, J.A., Peddle, D.R., 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., Gibeau, M.L., Herrero, S., 2005. Grizzly bear demographics in and around Banff National Park and Kananaskis Country, Alberta. Journal of Wildlife Management 69, 277–297.

Gibeau, M.L., 1998. Grizzly bear habitat effectiveness model for Banff, Yoho, and Kootenay National Parks, Canada. Ursus 10, 235–241.

Gibeau, M.L., Herrero, S., McLellan, B.N., Woods, J.G., 2001. Managing for grizzly bear security areas in Banff National Park and the Central Canadian Rocky Mountains. Ursus 12, 121–130.

Hamer, D., Herrero, S., 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., Herrero, S., Brady, K., 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.

Hobbs, N.T., Hanley, T.A., 1990. Habitat evaluation: do use/availability data reflect carrying capacity? Journal of Wildlife Management 54, 515–522.

Jacoby, M.E., Hilderbrand, G.V., Servheen, C., Schwartz, C.C., Arthur, S.M., Hanley, T.A., Robbins, C.T., Michener, R., 1999. Trophic relations of brown and black bears in several western

North American ecosystems. Journal of Wildlife Management 63, 921–929.

Johnson, C.J., Boyce, M.S., Schwartz, C.S., Haroldson, M.A., 2004. Modeling survival: applications of the multiplicative hazards model to Yellowstone grizzly bear. Journal of Wildlife Management 68, 966–978.

Knight, R.R., Eberhardt, L.L., 1985. Population dynamics of Yellowstone grizzly bears. Ecology 66, 323–334.

Knight, R.R., Blanchard, B.M., Eberhardt, L.L., 1988. Mortality patterns and population sinks for Yellowstone grizzly bears, 1973–1985. Wildlife Society Bulletin 16, 121–125.

Krebs, C.J., 1985. Ecology: The Experimental Analysis of Distribution and Abundance, third ed. Harper and Row, New York, USA.

Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J., Zuuring, H., 1996. Relationship among grizzly bears, roads and habitat in the Swan Mountains, Montana. Journal of Applied Ecology 33, 1395–1404.

Mace, R.D., Waller, J.S., Manley, T.L., Ake, K., Wittinger, W.T., 1999. Landscape evaluation of grizzly bear habitat in western Montana. Conservation Biology 13, 367–377.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies, second ed. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Mattson, D.J., Herrero, S., Wright, R.G., Pease, C.M., 1996. Designing and managing protected areas for grizzly bears: how much is enough? In: Wright, R.G. (Ed.), National Parks and Protected Areas: Their Role in Environmental Protection. Blackwell Science, Cambridge, MA, pp. 133–164.

Mattson, D.J., Merrill, T., 2002. Extirpations of grizzly bears in the contiguous United States, 1850–2000. Conservation Biology 16, 1123–1136.

McDonald, T.L., McDonald, L.L., 2002. A new ecological risk assessment procedure using resource selection models and geographic information systems. Wildlife Society Bulletin 30, 1015–1021.

McLellan, B.N., 1998. Maintaining viability of brown bears along the southern fringe of their distribution. Ursus 10, 607–611.

McLellan, B.N., Hovey, F.W., Mace, R.D., Woods, J.G., Carney, D.W., Gibeau, M.L., Wakkinen, W.L., Kasworm, W.F., 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. Journal of Wildlife Management 63, 911–920.

McLellan, B.N., Hovey, F.W., 2001. Habitats selected by grizzly bears in a multiple use landscape. Journal of Wildlife Management 65, 92–99.

Mladenoff, D.J., Sickley, T.A., Haight, R.G., Wydeven, A.P., 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes Region. Conservation Biology 9, 279–294.

Nams, V.O., Mowat, G., Panian, M.A., 2006. Determining the spatial scale for conservation purposes – an example with grizzly bears. Biological Conservation 128, 109–119.

Naves, J., Wiegand, T., Revilla, E., Delibes, M., 2003. Endangered species constrained by natural and human factors: the case of brown bears in northern Spain. Conservation Biology 17, 1276–1289.

Nielsen, S.E., 2005. Habitat ecology, conservation and projected population viability of grizzly bears (*Ursus arctos* L.) in west-central Alberta, Canada. Ph.D. Thesis, University of Alberta, Edmonton, Alta., Canada.

Nielsen, S.E., Boyce, M.S., Stenhouse, G.B., Munro, R.H.M., 2002. Modeling grizzly bear habitats in the Yellowhead Ecosystem of Alberta: taking autocorrelation seriously. Ursus 13, 45–56.

Nielsen, S.E., Boyce, M.S., Stenhouse, G.B., Munro, R.H.M., 2003. Development and testing of phenologically driven grizzly bear habitat models. Ecoscience 10, 1–10.

Nielsen, S.E., Herrero, S., Boyce, M.S., Mace, R.D., Benn, B., Gibeau, M.L., Jevons, S., 2004a. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies Ecosystem of Canada. Biological Conservation 120, 101–113.

Nielsen, S.E., Boyce, M.S., Stenhouse, G.B., 2004b. Grizzly bears and forestry I: selection of clearcuts by grizzly bears in west-central Alberta, Canada. Forest Ecology and Management 199, 51–65.

Nielsen, S.E., Munro, R.H.M., Bainbridge, E., Boyce, M.S., Stenhouse, G.B., 2004c. Grizzly bears and forestry II: distribution of grizzly bear foods in clearcuts of west-central Alberta. Forest Ecology and Management 199, 67–82.

Posillico, M., Meriggi, A., Pagnin, E., Lovari, S., Russo, L., 2004. A habitat model for brown bear conservation and land use planning in the central Apennines. Biological Conservation 118, 141–150.

Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000a. Predicting extinction risk in declining species. Proceedings of the Royal Society of London B 267, 1947–1952.

Purvis, A., Agapow, P.M., Gittleman, J.L., Mace, G.M., 2000b. Nonrandom extinction and the loss of evolutionary history. Science 288, 328–330.

Ratti, J.T., Reese, K.P., 1988. Preliminary test of the ecological trap hypothesis. Journal of Wildlife Management 52, 484–491.

Russell, G.J., Brooks, T.M., McKinney, M.M., Anderson, C.G., 1998. Present and future taxonomic selectivity in bird and mammal extinctions. Conservation Biology 12, 1365–1376.

Schirokauer, D.W., Boyd, H.M., 1998. Bear-human conflict management in Denali National Park and Preserve, 1982–94. Ursus 10, 395–403.

Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A., Samson, F.B., 2001. Introduction. In: Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M.G., Wall, W.A., Samson, F.B. (Eds.), Predicting Species Occurrences: Issues of Accuracy and Scale. Island Press, Washington, DC, USA, pp. 1–5.

Stenhouse, G.B., Boyce, M.S., Boulanger, J., 2003. Report on Alberta Grizzly Bear Assessment of Allocation. Alberta Sustainable Resource Development, Fish and Wildlife Division, Hinton, Alta.

Tardiff, S.E., Stanford, J.A., 1998. Grizzly bear digging: effects on subalpine meadow plants in relation to mineral nitrogen availability. Ecology 79, 2219–2228.

Tellez-Valdes, O., Davila-Aranda, P., 2003. Protected areas and climate change: a case study of the cacti in the Tehuacan-Cuicatlan biosphere reserve, Mexico. Conservation Biology 17, 846–853.

Theberge, J.C., 2002. Scale-dependent selection of resource characteristics and landscape pattern by female grizzly bears in the eastern slopes of the Canadian Rocky Mountains. Ph.D. dissertation, University of Calgary, Calgary, Alta., Canada.

Tyre, A.J., Possingham, H.P., Lindenmayer, D.B., 2001. Matching observed pattern with model process: can territory occupancy provide information about life history parameters. Ecological Applications 11, 1722–1737.

Van Horne, B., 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47, 893–901.

Waller, J.S., Mace, R.D., 1997. Grizzly bear habitat selection in the Swan Mountains, Montana. Journal of Wildlife Management 61, 1032–1039.

Wiegand, T., Naves, J., Stephan, T., Fernandez, A., 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the

Cordillera Cantabrica, Spain. Ecological Applications 68, 539–570.

Wielgus, R.B., Sarrazin, F., Ferriere, R., Clobert, J., 2001. Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. Biological Conservation 98, 293–303.

Woodruffe, R., 2000. Predators and people: using human densities to interpret declines of large carnivores. Animal Conservation 3, 165–173.

Yip, J.Y., Corlett, R.T., Dudgeon, D., 2004. A fine-scale gap analysis of the existing protected area system in Hong Kong, China. Biodiversity and Conservation 13, 943–957.