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Hibernation is an adaptive strategy to avoid harsh environmental conditions and seasonal limitations in food and water. Unlike most hibernators, grizzly bears (*Ursus arctos*) are aroused easily while in dens and disturbances while denning can result in fitness costs if bears become active during this period. Our objectives were to determine den selection of male and female grizzly bears at multiple spatial scales in the boreal forest and Rocky Mountains of Alberta, Canada. Grizzly bears in Alberta are designated as threatened. However, little is known about den selection by grizzly bears in the boreal forest and the current land and forest management plans do not include any mitigation measures to minimize possible impacts on the denning habitat of grizzly bears. We compared dens to random available locations within fall home ranges using geographic information system–derived anthropogenic, land cover, landscape, and food resource variables. Male and female grizzly bears had similar habitat requirements when selecting dens, and females did not avoid sites associated with a greater probability of encountering males. At the broadest scale investigated, grizzly bears avoided wetlands, and selected high-elevation, dry conifer stands with abundant high-quality spring food. At more localized scales, grizzly bears selected areas of low road densities and dense conifers associated with little high-quality autumn food. Slope angle had the most influence on den selection followed by percent autumn food, road densities, percent wetland, and percent spring food. We recommend limiting human disturbance, including open roads, within core grizzly bear conservation areas for areas with high suitable den habitat.

Key words: boreal forest, den selection, hibernator, spatial scales, *Ursus arctos*

Mammalian hibernation is viewed as an adaptive strategy to avoid seasonal scarcity of food and water and is characterized by periods of inactivity and metabolic suppression (Watts et al. 1981). By hibernating, mammals such as ground squirrels (*Spermophilus* spp.), marmots (*Marmota* spp.), and mice (e.g., *Perognathus* spp.) are able to reduce their energy expenditure to below 15% of what would be expended by remaining normothermic throughout the winter (Geiser 2004). Hibernation in bears (*Ursus* spp.) is unique in that bears lower their metabolic rate and body temperatures only slightly while hibernating, and they do not undergo deep torpor bouts typical of rodent hibernators (Watts et al. 1981). Unlike other hibernators, bats (e.g., *Myotis* spp.) and bears can be aroused easily while hibernating (Tietje and Ruff 1980; Boyles and Brack 2009). Disturbances while hibernating can alter energy savings (Tietje and Ruff 1980; Speakman et al. 1991) and reproductive outputs (Linnell et al. 2000), and can affect

survival rates (Boyles and Brack 2009), thereby reducing the benefits of hibernation.

Disturbances may have further negative effects in species for which reproductive timing and emergence from hibernation are closely linked. Little brown bats (*Myotis lucifugus*) and Richardson's ground squirrels (*Urocitellus richardsonii*) reproduce soon after winter emergence and the energy they allocate to reproductive outputs is directly linked to the energy expended during hibernation (Michener 1998; Humphries et al. 2003). Because bears give birth while in dens, cub loss from winter disturbance and den displacement can result in significant fitness costs (Tietje and Ruff 1980; Alt 1984; Swenson et al. 1997).

Considering the importance of hibernation in the life cycle of hibernating species, the habitat where hibernacula are located has the potential to have a profound impact on the success of hibernation. Consistent with the definition of "habitat" proposed by Hall et al. (1997), winter habitat for hibernators is the collection of resources (physical and vegetative) of their hibernacula and surrounding environment. The insulation properties, microclimate, and food resources available prior to, during, and after hibernation, the level of protection from predators, and the potential for natural or human-caused disturbances vary with the sites selected (Vroom et al. 1980; Birks et al. 2005). Previous research has shown that the availability and location of overwintering sites can be limiting resources and affect population distribution and abundance (Carey et al. 1997; Pyare et al. 2010). Availability of den sites also affects the shape and size of territories in some species, thereby affecting the quality and abundance of available food within individual home ranges (Doncaster and Woodroffe 1993). Therefore, to maximize fitness, hibernators should invest considerable efforts in the selection of overwintering sites.

In North America, grizzly bear (*Ursus arctos*) numbers have decreased substantially for more than a century (Mattson and Merrill 2002) and, even though populations in the contiguous United States are now increasing as a result of management actions (Mace et al. 2012), small and isolated populations are still currently threatened (McLellan et al. 2008; Nielsen et al. 2009; Mace et al. 2012). To date, conservation efforts have focused on the impacts of human activities (Nielsen et al. 2006, 2008; Coleman et al. 2013), and the spatial distribution and habitat selection of grizzly bears during the active season (e.g., Nielsen et al. 2004; Milakovic et al. 2012). Even though den selection by grizzly bears has been investigated in a variety of mountainous landscapes (e.g., Vroom et al. 1980; McLoughlin et al. 2002; Goldstein et al. 2010), den selection by grizzly bears in the boreal forest has never been investigated, and little is known about how winter requirements in mountain and foothill environments need to be incorporated into conservation and management efforts. In North America, black bears (*Ursus americanus*) and grizzly bears hibernate typically for 4–7 months (Judd et al. 1983; Haroldson et al. 2002; McLoughlin et al. 2002; Gaines 2003; Mitchell et al. 2005; Inman et al. 2007) and previous studies showed that grizzly bears dig dens commonly on steep slopes located at mid- to high elevations and farther from roads than randomly expected (Ciarniello et al. 2005; Goldstein et al. 2010). Similar findings, including avoidance of wet areas, have been observed for American black bears across North America (Smith et al. 1994; Gaines 2003; Mitchell et al. 2005; Reynolds-Hogland et al. 2007). Considering that the energy expended during hibernation is greater for lactating females than for other individuals (Tietje and Ruff 1980; Farley and Robbins 1995; López-Alfaro et al. 2013) and because in some populations, adult males are known to kill young cubs (Wielgus and Bunnell 2000; Bellemain et al. 2006), sexual segregation also may be important in den selection by bears (Manville 1987; Elfstrom and Swenson

2009; Libal et al. 2011). Avoidance of anthropogenic features by denning brown bears (*Ursus arctos*—e.g., Ciarniello et al. 2005; Elfstrom et al. 2008; Goldstein et al. 2010) and black bears (e.g., Gaines 2003; Reynolds-Hogland et al. 2007) has been documented in several instances but to our knowledge only Elfstrom et al. (2008) and Elfstrom and Swenson (2009) have investigated sex-specific differences related to anthropogenic features in brown bears. Elfstrom and Swenson (2009) observed that male brown bears denned farther from plowed roads than did other sex–age groups. Manville (1987) found that male black bears denned farther from sites associated with human activities than did females, and Reynolds-Hogland et al. (2007) found that females with cubs avoided roads more than did lone females. Because habitat selection can be scale dependent (Boyce 2006; Ciarniello et al. 2007), a thorough analysis of the scales at which individuals perceive and respond to their environment is necessary to identify factors affecting selection (Hobbs 2003; Mayor et al. 2009). Until now, the importance of different scales in the selection of dens by grizzly bears has not been considered. Commonly, it is accepted that selection occurring at broad scales limits the selection of habitat characteristics at finer scales (Rettie and Messier 2000; Boyce 2006) and this ecological process should be considered when investigating selection of overwintering sites (Henner et al. 2004; Crook and Chamberlain 2010). In the boreal forest, a major portion of industrial activities from timber harvesting and from oil and gas exploration takes place during winter and disturbances of grizzly bears at dens are common (Alberta Sustainable Resource Development, Fish and Wildlife Division 2008). In Scandinavia, European brown bears are sensitive to winter disturbances and, currently, no evidence suggests that grizzly bears in North America behave differently. In a recent study, 24 of 25 brown bears immobilized while denning abandoned their dens within a few days of the disturbances (Evans et al. 2012; A. Evans, Department of Forestry and Wildlife Management, Hedmark University College, Elverum, Norway & Norwegian School of Veterinary Science, Tromso, Norway, pers. comm.).

In 2010, grizzly bears in Alberta, Canada, were designated as a threatened species because of small population size, low reproductive rates, low immigration from adjacent populations, and high levels of human-caused mortality (Alberta Sustainable Resource Development and Alberta Conservation Association 2010). Currently, land and forest management planning in Alberta does not include any mitigation measures to minimize possible impacts on denning habitat of grizzly bears because little information is available to understand where and under what conditions grizzly bears den in boreal forests. Within the current recovery plan for grizzly bears in Alberta, the threshold values for open road densities within core priority areas and secondary habitats for grizzly bears are set at 0.6 km/km^2 and 1.2 km/km^2, respectively (Alberta Sustainable Resource Development, Fish and Wildlife Division 2008; Nielsen et al. 2009), but the effectiveness of these thresholds to reduce or limit human-caused mortality rates has not been evaluated. Understanding winter habitat requirements of

TABLE 1.—Working hypotheses and predictions proposed to identify factors determining den selection for male and female grizzly bears (*Ursus arctos*) at multiple spatial scales in the boreal forest and Rocky Mountains of Alberta, Canada. For each hypothesis and prediction, we first investigated differences between male and female den selection using univariate logistic regression (Supporting Information S4) and performed a 1st-step model selection on a set of bivariate models using conditional logistic regression (Table 4; Supporting Information S5). Based on the results from the bivariate model selection, we performed a 2nd-step (and final) model selection on a set of multivariate models using conditional logistic regression (Table 3; Supporting Information S6). Each model is associated with a hypothesis, a prediction, and categories of factors.

Hypothesis	Full description	Justification	Prediction[a]	Categories of factors
1) Den insulation	Grizzly bears select dens within topographic and habitat features that maximize the insulation properties of the den.	Reduce energy expenditure.	a) Avoid moist sites. b) Select sites with high snow retention.	Topography Land cover
2) Remoteness	Grizzly bears select dens that are away from anthropogenic disturbances and difficult to access.	High cost of disturbance.	a) Select sites difficult to access. Avoid areas with: b) High vehicle traffic. c) High forestry-related activities. d) High oil and gas-related activities.	Anthropogenic Topography
3) Food resources	To reduce energy expenditure, and for females, to reduce the probability of infanticide, grizzly bears select dens with high food resources and water.	Avoidance of infanticide and reduce energy expenditure.	a) Select dens with a high proportion of food and water. b) Females select dens with a high proportion of food and water.	Resources
4) Increased avoidance for females	Female grizzly bears avoid anthropogenic features more than males because of the high costs associated with cub loss following disturbance.	High cost of disturbance for pregnant or lactating females.	a) Females show a stronger avoidance of anthropogenic features than males. b) Females den in more remote sites than males.	Anthropogenic Topography

[a] Predicting an increase in the probability of den selection.

grizzly bears for this region will make possible the reduction of direct disturbances of grizzly bears while in dens and will enable land managers to consider reducing timber harvesting and oil and gas exploration activities and, therefore, road construction within high-quality areas for denning.

Our objectives were to determine the denning requirements of male and female grizzly bears in the Rocky Mountains and boreal forest of Alberta. We hypothesized that within their home ranges, grizzly bears select dens that are (1) well insulated and (2) away from human disturbances (Table 1). We also hypothesized that to reduce energy expenditure prior to and after den emergence, (3a) grizzly bears den in areas with abundant autumn or spring foods, or both. An alternative hypothesis is that (3b) only females select dens with abundant spring food and water so that they need not travel after den emergence, lowering the probability of encountering males. Also, because the energy costs incurred from disturbances and den abandonment for females are greater than for males (i.e., potential cub loss—Swenson et al. 1997; Linnell et al. 2000), we hypothesized a (4) stronger avoidance of anthropogenic features by females than by males. To test these hypotheses, we evaluated den selection at multiple spatial scales within 2 grizzly bear population units in Alberta, Canada, defined the relative probability of den selection from male and female grizzly bears, and delineated preferred sites within the study area.

MATERIALS AND METHODS

Study area.—We studied adult grizzly bears of both sexes between 2000 and 2011 in the core conservation areas for grizzly bears in the Grande-Cache and Yellowhead population units (Alberta Sustainable Resource Development 2010; Fig. 1). Both population units include protected and unprotected mountainous terrain (national and provincial parks) as well as rolling foothills (boreal forest) extensively altered by anthropogenic activities that are associated with forestry, coal mining, oil and gas exploration, and human recreational activities. The Grande-Cache population unit extends west from the British Columbia–Alberta border toward highway 40 (54°30′N, 119°6′W). Elevation varies from 543 to 2,440 m above sea level with upper and lower foothills dominating the area. Forests are primarily lodgepole pine (*Pinus contorta*), black spruce (*Picea mariana*), and white spruce (*Picea glauca*), but also with some areas of aspen (*Populus tremuloides*). The Yellowhead population unit, which is south of the Grande-Cache unit, extends west from the British Columbia–Alberta border toward the towns of Cadomin and Hinton (52°48′N, 117°7′W) and includes parts of Jasper National Park. Elevation varies from 712 to 3,680 m above sea level and is dominated by mountainous terrain. Dominant tree species are lodgepole pine, white spruce, and, at high elevation, subalpine fir (*Abies lasiocarpa*) and Englemann spruce (*Picea englemannii*). Although alpine areas have less industrial activity, they do experience significant recreational activities.

Den site location data.—We investigated the selection of 79 dens of 15 male and 35 female grizzly bears 4 years of age or older. We captured and collared bears between 2000 and 2011 using aerial darting, leghold snares, and culvert traps. Capture and handling techniques were in accordance with guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the University of Saskatchewan Animal
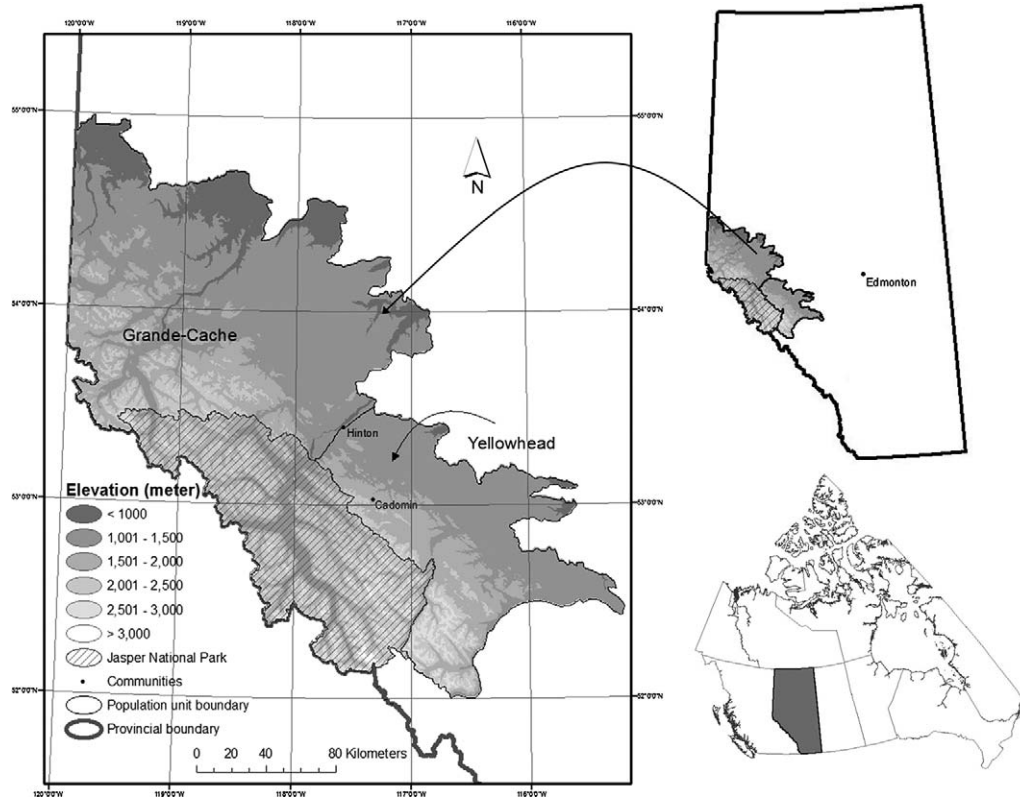
FIG. 1.—Overview of the study area in Alberta, Canada, showing elevation, the Grande-Cache provincial grizzly bear (*Ursus arctos*) population unit (north), the Yellowhead provincial grizzly bear population unit (south), and general location within Alberta. Jasper National Park is delineated by the hatched area.

Care Committee; Cattet et al. (2003) provided a full description of capture and handling techniques. We fitted bears with Advance Telemetry Systems (ATS, Isanti, Minnesota; 2000–2002) or Televilt Global Positioning System (Lindesberg, Sweden; 2000–2011) collars. We located dens using location data acquired from global positioning system collars while denning occurred. We travelled to and physically marked the locations of 44 dens with handheld global positioning system units and used the geographic center of the global positioning system–collar locations acquired during denning to define the location of the 35 other dens. Average global positioning system–collar location (centroid) was within 10 m ($SE = 3$ m) of the actual den location based on an evaluation of 44 visited dens using a handheld global positioning system unit. This error was much smaller than the raster cell size used in analyses. Mean error between the centroid of global positioning system–collar locations and the handheld global positioning system locations of physically located dens was 10 $\pm$ 3 m. Therefore, we considered the centroids of global positioning system–collar locations to represent the location of the 35 unvisited dens accurately.

Environmental factors.—To test our hypotheses, we generated geographic information system layers for 4 major factors related to our hypotheses (Tables 1 and 2). These factors included topography, land cover, anthropogenic features, and food resources. Attributes of these factors are described further in Table 2. We extracted values of diet-based habitat productivity from spring and autumn food-based habitat models of Nielsen et al. (2010). The food-based habitat models represent proportions of high-quality, seasonally important food, predicted at sites based on knowledge of species distribution models for individual bear food (Nielsen et al. 2010). To model values of spring and autumn food-based habitat, we used the 2 earliest and latest bimonthly periods assessed by Nielsen et al. (2010). These periods represent conditions shortly before denning and shortly after den emergence. Specifically, the spring bimonthly midpoints were 7 and 21 May, whereas the autumn midpoints were 7 and 21 September. We derived topographic factors including slope, hillshade, and terrain wetness based on the compound topographic index (Gessler et al. 2000) from a 30-m digital elevation model. Hillshade is a grid model showing the hypothetical illumination of a surface and terrain wetness is a grid model that considers the slope and drainage from upstream contributing areas. A snow load index (Table 2) was developed to take into account the influence of predominant wind direction and elevation on the snow load potential of slopes. Predominant winds in the study area are from the west and create deep snowpacks on high-elevation, east-facing slopes, whereas east-facing slopes are scoured. We edited a 30-m-resolution aspect grid to remove the circular nature of the grid and obtain values ranging between 0 and 180 for west- and

TABLE 2.—Factors used to assess den selection of grizzly bears (*Ursus arctos*) in the boreal forest and Rocky Mountains of Alberta, Canada, between 2000 and 2011. DEM = digital elevation model.

Category	Factors	Description	Range
Topography	Elevation	Elevation based on 30-m DEM (m)	752–2,822
	Slope	Slope (degree)	4.5–69.3
	Shade	Hillshade, considers illumination angle and shadow (degree)	0–254.0
	HLI	Heat load index, based on McCune and Keon (2002)[a]	1,201–5,760
	CTI	Compound topographic index[b]	2.6–14.8
	SRR	Surface relief ratio, a measure of rugosity	0.2–0.9
	SLI	Snow load index, considers prevailing winds and elevation	0–0.7
Land cover	Wetland	30-m pixels with presence of trees and open wetland (%)[c]	0–17.2
	Deciduous	30-m pixels with presence of deciduous trees (%)[c]	5.2–68.8
	Canopy	Average percentage of canopy cover (%)[c]	30.9–90.7
	Patch size	Size of continuous forest patch of observed locations (km^2)[d]	0–673.2
Anthropogenic features	Regeneration	30 m-pixels with the presence of young regenerating stands, 0–5 years (%)[c]	0–100
	Truck trails	Density of truck trails (km^2)[c]	0–0.5
	Roads	Density of moderate to heavy-use roads (km^2)[c]	0–3.8
	Well sites	Density of well sites (km^2)[c]	0–0.8
Food resources	Autumn food	Diet-based productivity values for the month of September (%)[e]	0–100
	Spring food	Diet-based productivity values for the month of May (%)[e]	0–100
	River	Distance to nearest river (km; 1:1,000,000 scale)	0–4.4
	Stream	Distance to nearest stream (km, 1:20,000 scale)	0–1.6

[a] Highest values are southwest and the lowest values are northeast; accounts for slope.
[b] A wetness index that considers the slope and upstream contributing area (Gessler et al. 2000).
[c] Within specified moving window.
[d] If the den or random location is not within a forested area, value is 0.
[e] Based on diet-based productivity values from Nielsen et al. (2010).

east-facing slopes while keeping north and south values identical. This modified aspect grid was then standardized between 0 and 1 with high values for east-facing slopes and low values for west-facing slopes. We also standardized an elevation digital elevation model between 0 and 1 with high grid values referring to high-elevation slopes. The product of the 2 standardized grids was used as the snow load index. East-facing, high-elevation slopes represented maximum snow load index values, whereas west-facing, low-elevation slopes represented minimum snow load index values. Finally, we distinguished truck trails from roads, and estimated well site densities from active well sites and thus did not consider reclaimed or abandoned (nonactive) wells.

Sampling intensity.—To investigate den selection at the home-range level we generated 95% kernel estimates of autumn home ranges using the program ABODE (Laver 2005) and used least-squares cross-validation to determine smoothing factors. We identified 16 August as the onset of hyperphagia following Nielsen's et al. (2006) delineation and used global positioning system locations of individual bears from the onset of hyperphagia to denning to determine autumn home ranges. Within each kernel estimate, we generated a sample of 100 random locations using ArcGIS 9.3 (Environmental Systems Research Institute [ESRI] 2008) and Hawth's Analysis Tools (Beyer 2004). We compared 100 random locations to each den location using conditional logistic regression (PROC PHREG—SAS Institute Inc. 2011) after evaluating the sensitivity of a subset of coefficients to an exponential range of random locations from 25 to 400. Coefficients did not vary by the number of random locations (up to 400) paired with dens (Supporting Information S1, DOI:

10.1644/13-MAMM-A-137.S1) with 100 random locations per home range used as a representative sample of available habitats within each home range. We chose to restrict random locations to areas with a minimum slope of 4.5° because previous studies on den selection found that bears do not den on flat ground (e.g., Elfstrom et al. 2008; Goldstein et al. 2010), and because the minimum 30-m digital elevation model slope associated with a den for our data set was 4.5°. Based on land cover classifications (Franklin et al. 2002) and the width of roads and oil and gas well sites measured using satellite imagery (SPOT5—BlackBridge Geomatic Corporation 2012), we excluded glaciers, roads, and oil and gas well sites from home ranges.

Sampling scales.—We allowed spatial scales to vary among variables because den selection could be constrained by factors acting at different spatial scales. For example, human disturbances such as timber harvesting, oil and gas activities, and roads can be perceived at broad and fine scales. High road densities within a small area around a potential den site (fine scale) might deter a bear from digging a den but unless different scales are investigated, it is impossible to know if the same density within a large area (broad scale) also is a deterrent. Topography, land cover, and human disturbance are heterogeneous in nature. We had little previous knowledge of the scales at which bears might perceive landscape factors and human disturbance while in dens; we therefore tested the sensitivity of the response variable (presence of dens) to an array of exponential scales for each covariate using a moving window analysis. We used mixed conditional logistic regression in SAS 9.3 (PROC PHREG with the STRATA and ID statements, and the COVSANDWICH[aggregate] and

TYPE = breslow options [SAS Institute Inc. 2011]) to compare dens with random locations. Model structure follows the log-linear form:

$$\pi(x_{njd}) = \frac{\int_J \exp(x'_{njd}\beta + z'_{njd}b)}{\sum_{i=1}^{J} \exp(x'_{nid}\beta + z'_{nid}b)}, \qquad (1)$$

where $\pi(x_{njd})$ represents the distribution function of the relative probability of den selection, $x'_{njd}\beta$ the regression coefficient for predictor x of individual n at den d with jth available locations, and $z'_{nid}b$ the animal-level independent random effects for individual n at den d with jth available locations and independent randomly distributed errors (Manly et al. 2002; Duchesne et al. 2010). We used the quasi-likelihood under the independence model criterion (QIC$_U$—Pan 2001) as a selection criterion because Akaike's information criterion is not applicable to generalized estimating equations because no likelihood is defined. For each of the factors, a unique scale was selected based on QIC$_U$ values and used in subsequent analyses (Boyce 2006). For fine scales (i.e., 0.15-km or 0.3-km scales), instances of perfect avoidance can be due to sample size rather than biological reasons; we therefore only included scales with at least 1 male and 1 female den in our models (Supporting Information S2 and S3, DOI: 10.1644/13-MAMM-A-137.S1). We tested exponential scales up to a 290-km^2 area (9.6-km-radius moving window), which represents the largest average daily movement rate observed for individuals in our study area (Graham and Stenhouse, in press). This scale also is larger than the average fall home range (200 km^2) calculated for bears in the study area; we therefore did not feel the need to consider larger spatial scales.

Sex differences.—We first used univariate logistic regression with a logit link and individual bears as repeated subjects in PROC GENMOD, SAS 9.3 (equation 2 [SAS Institute Inc. 2011]) to investigate potential differences in the selection of den factors (predictor variables) by males and females (binary response variable) while accounting for the correlation among different dens from the same individuals. Here $\pi(x)$ is the probability of being a male (0) or female (1), β_0 is the intercept, and $\beta_{1i}x_{1i}$ the regression coefficient for predictor x and individual i:

$$\pi(x_i) = e^{\exp}(\beta_0 + \beta_1 x_{1i} + \varepsilon_i)/[1 + e^{\exp}(\beta_0 + \beta_1 x_{1i} + \varepsilon_i)]. \qquad (2)$$

We interpreted significant coefficients as evidence of differences in male–female den selection for a particular factor. Female-based avoidance of male (Table 1, Food resources [3b]) could differ for females of different reproductive status. Therefore, we used univariate logistic regressions to investigate differences in the proportion of spring food near dens between males and females with cubs of the year, and between males and females with cubs of any age. We conducted analyses at the best selected scale for spring food (best QIC$_U$) and at the finest scale (0.15 km) because the finest scale best represents conditions at dens. For subsequent models, we included a sex-interaction term only for the factors showing evidence of male–female differences (Supporting Information S4, DOI: 10.1644/13-MAMM-A-137.S1).

Den site versus random locations within home ranges.—We used a case–control design and compared 100 random locations per home range to each den using mixed conditional logistic regression (equation 1). We used a relative probability function because our study design is based on used versus available resource units (Manly et al. 2002) and a conditional regression approach because using a single-point paired design would give an inappropriate representation of the availability of potential dens within home ranges, and available locations are unique for each individual based on home-range delineation. For 19 individuals, we observed more than 1 den and, therefore, accounted for the correlation among different dens from the same individuals (equation 1). Because even moderate collinearity can be problematic when investigating ecological signals, we removed any variable with a variance inflation factor higher than 3 prior to model building (Zuur et al. 2010).

A careful a priori consideration of a short list of candidate models is advocated when using an approach based on information-theoretic model selection (Burnham and Anderson 2002). To reduce the number of plausible candidate models and to avoid overparameterization, we used a 2-step model selection approach with multiple working hypotheses (Table 1). As a 1st step, we tested a suite of bivariate models using a maximum of 2 variables per model within each of the 4 major factors and ranked these bivariate models according to QIC$_U$ values and QIC$_U$ weights (Supporting Information S5, DOI: 10.1644/13-MAMM-A-137.S1). As a 2nd step, we used the best bivariate models obtained from the 1st step to build a 2nd set of candidate models (multivariate models) using a mix of variables across categories for the final model selection (Burnham and Anderson 2002; Supporting Information S6, DOI: 10.1644/13-MAMM-A-137.S1). All bivariate and multivariate candidate models were relevant biologically and associated with a hypothesis and prediction, or a combination of non–mutually exclusive hypotheses (Table 3; Supporting Information S5 and S6). The multivariate model with the lowest delta QIC$_U$ value and highest QIC$_U$ weight best described the probability of den selection.

Resource selection functions.—Using the final model (the best model from the multivariate model selection), we generated a map of the relative probability of den selection (i.e., a resource selection function). This map delineates high-quality denning habitat and can be used to mitigate land-use impacts, and to evaluate the effect of open road densities on high-quality denning habitat in the area. Originally, we conducted analyses and generated separate resource selection function models for low-elevation (boreal forest) bears versus high-elevation mountain bears but models for the 2 regions were similar (Pigeon 2012). Therefore, we merged all data and present results from a single resource selection function model.

We first tallied the relative probability of den selection from our best model into 12 categories based on quantiles, and then

Tᴀʙʟᴇ 3.—Quasi-likelihood under the independence model criterion (QIC_U), delta QIC_U (ΔQIC_U), QIC_U weights (ω_i), and k (number of variables) for the multivariate candidate models investigating the selection of dens by female and male grizzly bears in the boreal forest and Rocky Mountains of Alberta, Canada, using conditional logistic regression. Best model ($\leq 2 \Delta QIC_U$) is in boldface type. Predictions are from hypotheses (1) den insulation, (2) remoteness, and (3) food resources. See Table 1 for a complete description of each hypothesis and prediction. Because of collinearity (variance inflation factor > 3) between elevation and spring food, elevation (highest variance inflation factor) was removed from models including spring food. Model selection using elevation instead of spring food yields similar results (Supporting Information S6).

Predictions	Model	k	QIC_U	ΔQIC_U	ω_i
Difficult human access, high snow retention, avoidance of moist soil, avoidance of traffic, and high food availability.	**Slope, wetland, deciduous, roads, spring and autumn food**	**6**	**658.79**	**0.00**	**0.94**
Difficult human access, avoidance of traffic, and high food availability.	Slope, roads, spring and autumn food	4	664.79	6.00	0.05
Difficult human access, high snow retention, avoidance of moist soil, and high food availability.	Slope, wetland, deciduous, spring and autumn food	5	667.79	9.01	0.01
High snow load, difficult human access, high snow retention, avoidance of moist soils, and avoidance of traffic.	Elevation, slope, wetland, deciduous, roads	5	670.39	11.61	0.00
High snow retention and avoidance of moist soils, avoidance of traffic, and high food availability.	Wetland, deciduous, roads, spring and autumn food	5	673.92	15.13	0.00
Difficult human access and high food availability.	Slope, spring and autumn food	3	674.91	16.12	0.00
High snow load, difficult human access, and avoidance of traffic.	Elevation, slope, roads	3	680.13	21.34	0.00
Difficult human access, high snow load, high snow retention, and avoidance of moist soil.	Elevation, slope, wetland, deciduous	4	681.44	22.66	0.00
Avoidance of traffic and high food availability.	Roads, spring and autumn food	3	682.88	24.09	0.00
High snow retention, avoidance of moist soil, and high food availability.	Wetland, deciduous, spring and autumn food	4	684.24	25.45	0.00
High snow retention, avoidance of moist soil, and avoidance of traffic.	Wetland, deciduous, roads	3	691.73	32.94	0.00
Difficult human access and high snow load.	Elevation, slope	2	693.70	34.91	0.00
High food availability.	Spring and autumn food	2	694.69	35.90	0.00
High snow retention and avoidance of moist soil.	Wetland, deciduous	2	705.31	46.52	0.00
Avoidance of traffic.	Truck trails, roads	2	710.94	52.15	0.00

recategorized the probabilities into 7 bins so that selection increased significantly between each successive bin (Nielsen et al. 2010). To assess the descriptive performance of our model, we used a modified k-fold cross-validation method adapted for case–control designs based on Fortin et al. (2009). In our case–control design, individual strata are composed of 1 observed den location and 100 random potential locations. We first generated the model using 80% of randomly selected strata and then estimated relative probabilities for the remaining 20% of the strata. For each stratum, the relative probability of observed location was ranked against the relative probability of its associated 100 random locations. We grouped all probabilities into 10 ranked categories and performed Spearman rank correlation between categories and associated frequencies (Boyce et al. 2002). We repeated this process 100 times and reported the mean and range of correlations (Fortin et al. 2009). We performed the same method using random locations only. For this, we compared the relative probability of 1 randomly selected location to the relative probabilities of the 99 remaining potential locations and grouped all relative probabilities into 10 ranked categories. Spearman rank correlation was again performed between categories and associated frequencies and this process was repeated 100 times (Fortin et al. 2009). A descriptive model should demonstrate high r_s-value when compared to a random pattern of selection (Boyce et al. 2002). Using 12 new den locations gathered in 2012, we also performed a Fisher's exact test (PROC FREQ with the exact chisq option—SAS Institute Inc. 2011) to evaluate the

performance of the model by comparing 2012 den locations to the expected bin frequencies based on model probabilities (Johnson et al. 2006).

Rᴇsᴜʟᴛs

Sampling scales.—Sampling scales revealed that no bear denned closer than 0.3 km from a well site or 0.15 km from roads and truck trails. We found no evidence of any further effect of well sites or truck trails on den site selection (Supporting Information S2 and S3). For each factor, the best selected models based on QIC_U ranks are illustrated in Supporting Information S2 and full rankings are available in Supporting Information S3. Land cover variables (deciduous and wetland) were best considered at broad spatial scales (4.8 km and 9.6 km, respectively), whereas anthropogenic features (roads) were best considered at a finer spatial scale (0.6 km). Sampling scales for spring and autumn food differed considerably; the best model for autumn food was the 0.15-km scale, whereas the best model for spring food was the 9.6 km scale (Supporting Information S2).

Sex differences.—Contrary to our hypotheses related to female-based male avoidance (hypothesis [3b]) and female-avoidance of anthropogenic features (hypothesis [4]; Table 1), females did not select habitats differently than males, and females with or without cubs did not avoid anthropogenic features more than did males (Supporting Information S4; all Ps > 0.1). Avoidance of well sites, roads, truck trails, and

TABLE 4.—Quasi-likelihood under the independence model criterion (QIC$_U$), delta QIC$_U$ (ΔQIC$_U$), QIC$_U$ weights (ω$_i$), and k (number of variables) for the most-supported (≤ 10 ΔQIC$_U$) bivariate candidate models per category of factors for the selection of dens by female and male grizzly bears in the boreal forest and Rocky Mountains of Alberta, Canada. Factor categories are (1) topography, (2) land cover, (3) anthropogenic features, and (4) food resources. See Table 1 for a full description of hypotheses and predictions, and Supporting Information S5 for the complete set of candidate models. Best models (≤ 2 ΔQIC$_U$) are in boldface type.

Category	Hypothesis	Prediction[a]	Model	k	QIC$_U$	ΔQIC$_U$	ω$_i$
Topography	**(2) Remoteness**	**Difficult human access**	**Elevation, slope**	**2**	**693.70**	**0.00**	**0.71**
	(2) Remoteness	Difficult human access	Slope	1	696.39	2.69	0.19
	(2) Remoteness	Difficult human access	Slope, surface relief ratio	2	697.54	3.84	0.10
Land cover	**(1) Den insulation**	**Avoidance of moist soil and high snow retention**	**Wetland, deciduous**	**2**	**705.31**	**0.00**	**0.90**
	(1) Den insulation	Avoidance of moist soil and high snow retention	Wetland, canopy	2	711.18	5.87	0.05
	(1) Den insulation	Avoidance of moist soil	Wetland	1	711.28	5.97	0.05
Anthropogenic	**(2) Remoteness**	**Avoidance of traffic**	**Roads**	**1**	**710.94**	**0.00**	**0.38**
	(2) Remoteness	**Avoidance of oil and gas activities**	**Truck trails, roads**	**2**	**711.96**	**1.02**	**0.23**
	(2) Remoteness	**Avoidance of forestry-related activities**	**Regeneration, roads**	**2**	**712.20**	**1.26**	**0.20**
	(2) Remoteness	**Avoidance of traffic**	**Well sites, roads**	**2**	**712.30**	**1.36**	**0.19**
Food resources	**(3) Resources**	**High food availability**	**Spring and autumn food**	**2**	**694.69**	**0.00**	**0.68**
	(3) Resources	**High food and water availability**	**Autumn food, rivers and streams**	**3**	**696.61**	**1.92**	**0.26**
	(3) Resources	High autumn food availability	Autumn food	1	699.41	4.71	0.06

[a] Predicting an increase in the probability of den selection.

young clear-cuts was the same for both sexes (Supporting Information S4). Males, however, were more likely to den in large contiguous forest patches (patch size; β: −0.01 ± 0.002, Z-score: −3.27, P = 0.001; Supporting Information S4). Females, on the other hand, were more likely than males to den in wet terrain microsites (high terrain wetness) representing landscape depressions and drainages (compound topographic index; β: 0.45 ± 0.19, Z-score: 2.35, P = 0.02; Supporting Information S4). No difference existed in the proportion of spring food near dens between males and females with cubs of the year (9.6 km; β: −0.8 ± 1.5, Z-score: −0.54, P = 0.6; 0.15 km; β: −0.9 ± 0.7, Z-score: −1.18, P = 0.2) and between males and females with cubs of any age (9.6 km; β: −0.8 ± 1.6, Z-score: −0.52, P = 0.6, 0.15 km; β: −1.0 ± 0.8, Z-score: −1.31, P = 0.2).

Den site versus random locations within home ranges, bivariate model selection.—Topography and land cover factors had much higher model support than did any of the other candidate models (Table 4). For the topography factors, the evidence ratio between the best model that included elevation and slope as covariates and the next best candidate model that only included slope was 3.7. The evidence ratio for the best land cover model including percent wetland and deciduous as covariates and the next best model that included percent wetland and canopy cover was 18. For anthropogenic factors, 4 top models were competing, and for the food resource category 2 models were competing (Table 4). Evidence ratios for the best anthropogenic model that only included road densities as a covariate and the next best candidates were 1.7 (model covariates: truck trails and roads), 1.9 (model covariates: regeneration and roads), and 2.0 (model covariates: well sites and roads). Although support for the best model was weak, the next best candidate models all included road densities and either truck trail densities, percent regenerating stands, or well site densities as covariates, whereas the best model only

included road densities. Therefore, the roads model was the best, most-parsimonious model within this category. For the food resource category, the evidence ratio for the best model that included percent spring and autumn food as covariates and

TABLE 5.—Parameter estimates (β), standard errors (*SE*), chi-square (χ^2), and *P*-values for the top competing bivariate models (≤ 2 ΔQIC$_U$, where QIC$_U$ is quasi-likelihood under the independence model criterion) in the 4 categories of factors for the selection of dens by female and male grizzly bears in the boreal forest and Rocky Mountains of Alberta, Canada. We only included the variables from the best bivariate models in the multivariate model selection process (2nd step).

Model	Parameter	β	*SE*	χ^2	*P*
Topography					
Model 1	Slope	0.06	0.01	28.5	< 0.0001
	Elevation	0.001	0.0004	8.0	0.005
Anthropogenic features					
Model 1	Roads	−2.2	0.6	13.3	0.0003
	ΔQIC$_U$ ≤ 2				
Model 2	Roads	−2.2	0.6	13.3	0.0003
	Truck trails	−1.2	1.4	0.7	0.4
Model 3	Roads	−2.2	0.6	14.0	0.0002
	Regeneration	−0.005	0.007	0.4	0.5
Model 4	Roads	−2.1	0.6	13.9	0.0002
	Well sites	−2.7	2.9	0.9	0.4
Land cover					
Model 1	Wetland	−1.2	0.4	8.5	0.004
	Deciduous	−0.06	0.02	6.7	0.01
Food resources					
Model 1	Autumn food	−0.02	0.01	21.6	< 0.0001
	Spring food	0.03	0.01	6.9	0.01
	ΔQIC$_U$ ≤ 2				
Model 2	Autumn food	−0.02	0.01	17.2	< 0.0001
	Rivers	−1.7	0.9	3.6	0.06
	Streams	0.2	0.2	1.9	0.2

the next candidate model that included percent autumn food and distance to rivers and streams as covariates was 2.6. The most-parsimonious model was the spring and autumn food model (Table 4). For the anthropogenic and food resources categories, we chose to include only the most-parsimonious models in the next step of the model selection process. When looking at categories of factors separately, grizzly bears selected dens that were in steep slopes at high elevations, dry conifer stands, areas farther from roads, and areas with low amounts of high-ranked autumn food and high proportions of high-ranked spring food (Table 5).

Den site versus random locations within home ranges, multivariate model selection.—The most-parsimonious multivariate model describing selection of den sites for male and female grizzly bears was our global model (Table 3). Because elevation had a variance inflation factor greater than 3 when included with spring food, we conducted model selection with either elevation or spring food in the models and found that the results were similar (Supporting Information S6). Here we present results without the elevation variable (Table 3). To dig their dens, grizzly bears selected steep slopes away from wetlands and roads that had little high-quality autumn food and abundant high-quality spring food (Fig. 2). The most-supported model had a weight of 94% and was superior to any other models (Table 3). Using coefficients from the most-supported multivariate model, we described the relative probability of den selection (i.e., a resource selection function [Table 6; Fig. 3]). Means and ranges of the Spearman rank correlations were 0.72 (−0.07–1.00) and 0.03 (−0.82–0.73) for observed and random locations, respectively, using k-fold cross-validation. Grizzly bears were more than 11 times more likely to select areas identified with the highest resource selection function value (bin 6) than areas that were attributed to the lowest resource selection function value (bin 1 [Table 6]). Fisher's exact test yielded no difference between the 2012 den locations and expected bin frequencies calculated from the model (χ^2_5: 4.2, P = 0.4), indicating good model fit. Based on likelihood ratios, slope had the most influence on the selection of dens followed by percent autumn food, road density, percent wetland, and percent spring food (Table 7; Fig. 2).

DISCUSSION

Using 11 years of grizzly bear denning data in the boreal forest and Rocky Mountains of Alberta, we demonstrated that male and female grizzly bears selected similar environments for dens, and that consistent with the understanding that landscape-scale selection may limit fine-scale selection (Rettie and Messier 2000), grizzly bears seemed to select habitat factors for denning at 2 spatial scales. Grizzly bears first selected broad high-elevation, dry, open conifer stands with abundant high-quality spring food to dig their dens. Within these stands, they then selected for sites with low road densities and dense conifers associated with few high-quality autumn food resources. Overall, our results suggest that den selection by grizzly bears is governed by both broadscale and fine-scale
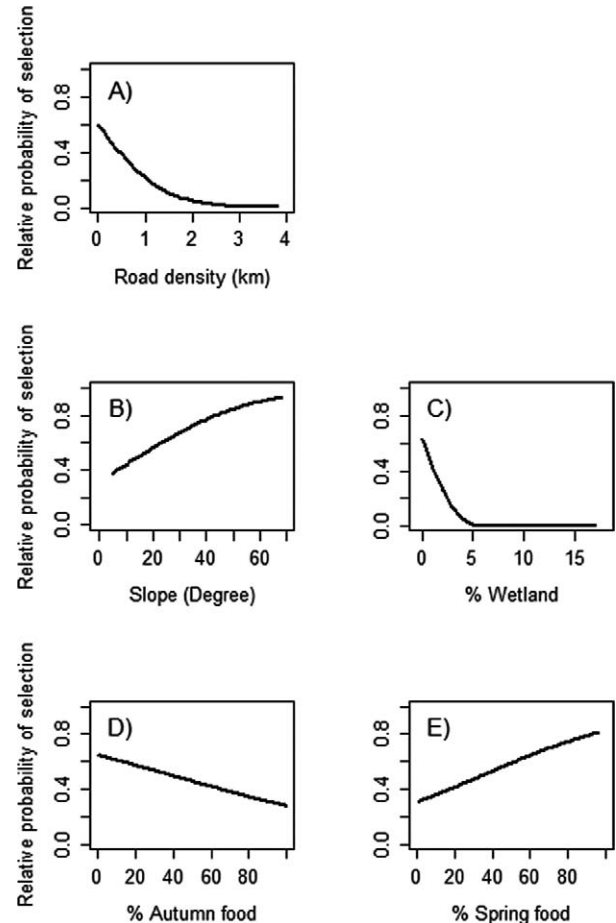

FIG. 2.—Relative probability of den selection of the most-supported multivariate model (Table 7) of den selection by male and female grizzly bears (*Ursus arctos*) in the boreal forest and Rocky Mountains of Alberta, Canada, between 2000 and 2011. A) Road density (km^2) at the 0.6-km scale, B) slope (degree), C) percent wetland at the 9.6-km scale, D) percent autumn food at the 0.15-km scale, and E) percent spring food at the 9.6-km scale. Each predictor variable is plotted within its observed range while other variables are held constant at their respective mean.

variables linked to den insulation, remoteness, and availability of spring food resources.

Our study is unique in that scales of perception had never been considered in the context of denning for grizzly bears and very few studies have considered scales for overwintering sites in other species (but see Henner et al. 2004; Crook and Chamberlain 2010; De Boer et al. 2013). Integrating scales in our analyses offered further insight into selection patterns and our findings provide land managers with information on the appropriate scale at which to implement mitigation measures. Researchers investigating selection of winter sites for any species should benefit from considering multiple spatial scales in their analyses.

As expected (Table 1), and consistent with findings on brown bears (Elfstrom et al. 2008) and black bears (Smith et al. 1994), grizzly bears in our study area maximized the insulation properties of dens by avoiding areas of water-saturated soils

TABLE 6.—Proportions of available area (a_i), proportion of dens (u_i), selection ratio ($w_{(x)}$), and risk ratio (RR) per bin of relative probability of den selection from the best multivariate model for male and female grizzly bears in the boreal forest and Rocky Mountains of Alberta, Canada.

Bin	a_i	Dens	u_i	$w_{(x)}$	Selection	RR[a]
0	0.00	0	0.00	0.00	Nonhabitat	0.00
1	0.14	3	0.04	0.28	Highly avoided	1.00
2	0.01	1	0.01	0.91	Slightly avoided	3.25
3	0.10	4	0.05	1.16	Slightly selected	4.15
4	0.26	16	0.20	1.58	Selected	5.66
5	0.25	24	0.30	2.45	Moderately selected	8.79
6	0.25	31	0.39	3.21	Highly selected	11.51

[a] Risk ratio is expressed relative to bin 1.

because nonsaturated soils provide better insulation. When a minimal percentage (6%) of the land cover surface was classified as wetland within a 9.6-km radius, the relative probability of selection dropped to 0. Grizzly bears did not, however, select deciduous stands even though deciduous forests could augment the insulation properties of dens because the reduced canopy cover in winter allows more snow to accumulate on the ground. Because deciduous forests are associated with low elevations in our study area, forests dominated by deciduous trees likely do not provide adequate snow conditions: frequent melt–freeze associated with low-elevation sites would reduce the insulation properties of the dens and this may explain why deciduous forests were not selected. Bears that had access to high-elevation sites also preferred to den on high ground. Denning at high elevation would increase snow load and augment the insulation properties of dens (Vroom et al. 1980). Although bears did select high-elevation sites, models predicting the selection for high snow load received little support (Supporting Information S5). It may be that any site above a certain elevation provides adequate snow for insulation and that other site factors such as aspect and prevailing winds may become unimportant once a critical elevation is attained (Vroom et al. 1980). Still, because snow load models received little support, we cannot rule out site remoteness or human avoidance rather than den insulation as possible explanations for the selection of high-elevation sites for denning. To shed light on the relative importance of site remoteness and den insulation as drivers of den selection for bears, future research should investigate the influence of snow depth on den selection.

As hypothesized (Table 1), grizzly bears selected sites away from anthropogenic disturbances and sites that are difficult for humans to access to dig their dens. Grizzly bears preferred steep slopes that are difficult to access and the relative probability of selection doubled when slope increased from 10° to 60°. The relative probability of den selection dropped by 30% when increasing road densities from 0 to 0.6 km/km^2 and by nearly 70% at road densities of 1.2 km/km^2. Once road densities reached 2.0 km/km^2, selection was nearly zero. We found no dens within 0.3 km of any oil and gas well sites. Forestry-related activities did not appear to influence den selection, although no dens were located in young clear-cuts. To insure availability of high-quality habitat for denning, and to reduce the potential for disturbances at dens, road densities in these high-quality habitats

should be kept at, or below, 0.6 km/km^2 and incorporated within the core priority areas for grizzly bears.

Although percent autumn food was more influential than spring food based on likelihood ratios, spring and autumn food had similar but inverse effects at their respective scales (Table 7; Fig. 2). With nearly linear relationships, a 20% decrease in autumn food within 0.15 km^2 of the den resulted in a 15% increase in the relative probability of selection, whereas a 20% increase in spring food within a 9.6-km radius was associated with an augmentation of about 25% in relative selection. Because the habitat productivity model we used as a surrogate for the presence of high-quality spring food is based on the predicted distribution (presence–absence) of food items weighted by seasonal diets, it reflects potential habitat productivity rather than the actual mapped presence of the foods (Nielsen et al. 2010). At the broadest scale evaluated (9.6 km), bears selected for sites (pixels) with a high proportion of
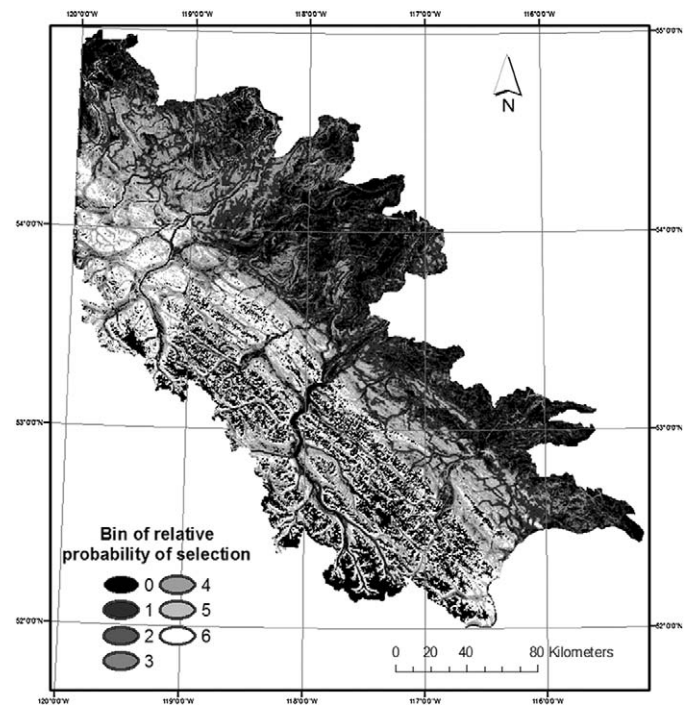

FIG. 3.—Relative probability of den selection based on the most-supported multivariate model (Table 7) of den selection by male and female grizzly bears (*Ursus arctos*) in the boreal forest and Rocky Mountains of Alberta, Canada, between 2000 and 2011.

TABLE 7.—Standardized parameter estimates (β), standard errors (*SE*), chi-square (χ^2), and *P*-values of the best multivariate model for the selection of dens by female and male grizzly bears in the boreal forest and Rocky Mountains of Alberta, Canada. Parameters are ranked in order of effect size based on likelihood ratio tests (LR χ^2).

Parameter	β	*SE*	χ^2	*P*	LR χ^2
Slope	0.05	0.01	24.86	< 0.0001	16.5
Autumn food	−0.02	0.01	8.99	0.003	11.6
Roads	−1.69	0.50	11.33	0.0008	9.9
Wetland	−0.84	0.36	5.50	0.02	7.8
Spring food	0.02	0.01	4.40	0.04	4.0
Deciduous	−0.02	0.02	1.17	0.3	1.2

high-quality spring food. These sites are associated with high-elevation, open conifer stands, and riparian habitats. At the finest scale investigated (0.15 km), the observed avoidance of autumn food could be due to the avoidance of habitat-specific factors associated with the presence of autumn food rather than the avoidance of the food itself. Future research would therefore benefit from field-based quantification of presence and abundance of food items near dens.

Contrary to our hypotheses (Table 1), female grizzly bears in our study area did not avoid sites associated with a greater probability of encountering males (Supporting Information S4), and did not avoid anthropogenic features more than males. Elevation of male and female dens did not differ and restricting the analysis to mountain-dwelling bears did not change the results (Supporting Information S7, DOI: 10.1644/ 13-MAMM-A-137.S1). In accordance with the findings of Elfstrom et al. (2008), who did not find differences in road avoidance by sex, we found no difference in the density of roads, truck trails, well sites, or young regenerating stands surrounding dens of male and female grizzly bears, and of females of different reproductive status. Both sexes avoided areas of high road densities to dig their dens (Fig. 2). It is possible that even if the potential cost of disturbance while denning is greater for females than males, females do not need to select different dens than males because both sexes effectively perceive anthropogenic features as threats. In future studies, measures of habitat quality that account for the impacts of human disturbances at dens and their potential effects on the reproductive success of females should be investigated.

Conclusions and management implications.—Many industrial activities and human recreational pursuits take place within grizzly bear habitat during the winter. Our findings can be used to develop guidelines to minimize human–bear interactions and the potential impacts of land-use activities on occupied and potential denning habitat for grizzly bears. Preserving high-quality habitat for denning can be considered as a potential management tool because grizzly bears prefer and avoid specific landscape and land cover features when selecting dens. We recommend including areas of high relative probability of den selection within core priority areas delineated for grizzly bears (Nielsen et al. 2009), because this should limit open road densities and road development, and therefore help recovery efforts. Temporary winter road closures in high-quality habitat for denning also could be considered as a management action to reduce potential disturbances at dens. Forest harvest planning should take into account the identified habitat characteristics needed for grizzly bear denning and seek to limit disturbances at dens. Den surveys should be conducted in areas of high probability of den selection prior to the onset of winter activities. Results from this research are important in understanding denning requirements of grizzly bears in the boreal forest while our analytical approach using multiple scales remains applicable to a broad range of hibernators and other areas.

SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—Evaluation of the sensitivity of conditional logistic regression to different numbers of random locations.
Found at DOI: 10.1644/13-MAMM-A-137.S1 (56 KB DOCX)
SUPPORTING INFORMATION S2.—Scales of factors selected.
Found at DOI: 10.1644/13-MAMM-A-137.S1 (56 KB DOCX)
SUPPORTING INFORMATION S3.—Parameter estimates for scale-based candidate models.
Found at DOI: 10.1644/13-MAMM-A-137.S1 (56 KB DOCX)
SUPPORTING INFORMATION S4.—Parameter estimates used to determine differences in selection between males and females.
Found at DOI: 10.1644/13-MAMM-A-137.S1 (56 KB DOCX)
SUPPORTING INFORMATION S5.—Parameter estimates for bivariate candidate models proposed to identify the selection of dens.
Found at DOI: 10.1644/13-MAMM-A-137.S1 (56 KB DOCX)
SUPPORTING INFORMATION S6.—Parameter estimates for multivariate candidate models proposed to identify the selection of dens.
Found at DOI: 10.1644/13-MAMM-A-137.S1 (56 KB DOCX)
SUPPORTING INFORMATION S7.—Parameter estimates for logistic regression used to determine differences in the selection of elevation.
Found at DOI: 10.1644/13-MAMM-A-137.S1 (56 KB DOCX)

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