Polar bear (*Ursus maritimus*) maternity denning habitat in western Hudson Bay: a bottom-up approach to resource selection functions

Evan Richardson, Ian Stirling, and David S. Hik

Abstract: We examined habitat characteristics of 101 polar bear (*Ursus maritimus* Phipps, 1774) den sites and 83 adjacent unoccupied sites in western Hudson Bay, Canada, between mid-August and early October 2001 and 2002. Bears denned almost exclusively in peat banks (n = 100) along the edges of creeks, rivers, and lakes adjacent to open lichen tundra sites. Den sites differed from unoccupied sites by having greater tree cover (P = 0.002), less moss cover (P < 0.001), and less herbaceous cover (P = 0.005). The presence of tree roots improved substrate stability, providing support to den structures. Den entrance azimuths were weighted toward a southeasterly aspect (P < 0.005), away from the prevailing northwest winds. To identify habitats with the greatest relative probability of having a den, a resource selection function (RSF) model was developed using remote sensing imagery and 1245 known den locations. High normalized difference vegetation index and brightness values derived from Landsat imagery, which were in close proximity to water, corresponded well with polar bear den sites. Identification of critical denning areas through the use of RSF will provide resource managers with a valuable tool for ensuring the protection of denning habitat, and consequently female bears and their young.

Résumé : Nous avons examiné, dans l'ouest de la Baie d'Hudson, Canada, les caractéristiques des habitats de 101 sites de terriers d'ours polaires (*Ursus maritimus* Phipps, 1774) et de 83 sites adjacents inoccupés entre la mi-août et de début d'octobre en 2001 et 2002. Les ours font leurs terriers presque exclusivement dans des talus tourbeux (n = 100) sur les berges de ruisseaux, de rivières et de lacs adjacents à des sites de toundra ouverte à lichens. Les sites des terriers diffèrent des sites inoccupés par une plus grande couverture d'arbres (P = 0,002) et des couvertures réduites de mousses (P < 0,001) et de plantes herbacées (P = 0,005). La présence de racines d'arbres augmente la stabilité du substrat en fournissant un support aux structures du terrier. Les entrées des terriers sont surtout orientées en direction sud-est (P < 0,005), à l'abri des vents dominants de direction nord-ouest. Afin d'identifier les habitats avec la plus grande probabilité relative de contenir un terrier, nous avons mis au point un modèle contenant une fonction de sélection des ressources (RSF) à l'aide d'images obtenues par télédétection et des coordonnées connues de 1245 terriers. Les valeurs élevées de l'indice de végétation par différence normalisée et les valeurs fortes de brillance obtenues par imagerie Landsat, qui se situent près de l'eau, correspondent bien aux sites des terriers des ours polaires. L'utilisation de la RSF pour l'identification des sites essentiels des terriers fournira aux gestionnaires un outil précieux pour assurer la protection des habitats propices aux terriers et, par ricochet, celle des ourses et de leurs petits.

[Traduit par la Rédaction]

Introduction

Over most of their circumpolar range, female polar bears (*Ursus maritimus* Phipps, 1774) dig snow dens in which to give birth and nurture their young. These parturition sites provide protection from cold temperatures and are important for the survival and development of cubs (Blix and Lentfer 1979). While some female bears may occupy maternity dens on drifting sea ice in the Beaufort Sea (Lentfer 1975; Amstrup and Gardner 1994), almost all known maternity dens in Canada (Harington 1968; Ramsay and Stirling 1990; Stirling and Andriashek 1992; Messier et al. 1994; Ferguson et al. 1997), Svalbard (Larsen 1985; Wiig 1995), Greenland (Born et al. 1997), and the Russian Arctic (Uspenski and Kistchinski 1972; Garner et al. 1990) have been found in drifted snow banks on land. Because female bears show fidelity to terrestrial denning areas (Ramsay and Stirling 1990; Amstrup and Gardner 1994; Scott and Stirling 2002), considerable efforts have been made to document the distribution of den sites (e.g., Van de Velde et al. 2003).

The distribution of den sites is a function of several factors including the availability of suitable denning habitat (i.e., snowdrifts), sea ice conditions, den site fidelity, and anthropogenic influences (Schweinsburg 1979; Belikov

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E. Richardson,[1,2] I. Stirling,[2] and D.S. Hik. University of Alberta, Department of Biological Sciences, Edmonton, AB T6G 2E9, Canada.

[1]Corresponding author (e-mail: Evan.Richardson@ec.gc.ca).
[2]Present address: Canadian Wildlife Service, 5320-122 Street, Edmonton, AB T6H 3S5, Canada.

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1980; Lentfer and Hensel 1980; Hansson and Thomassen 1983; Stirling and Andriashek 1992). Throughout most of the Arctic, dens are distributed at relatively low densities (Stirling et al. 1984), with the exception of high concentrations of dens in western Hudson Bay, Svalbard, and Wrangel Island (Uspenski and Kistchinski 1972; Stirling et al. 1977; Larsen 1985). Protection of denning areas is essential, as disturbance of bears in maternal dens may result in den relocation or abandonment of dens and reduced survival of young (Ramsay and Stirling 1986; Amstrup and Gardner 1994; Durner et al. 2003; Lunn et al. 2004).

In most areas, successful denning requires sufficient accumulation of snow, such that a pregnant female can dig a snow cave early in the winter and remain covered (Amstrup 2003). However, at the southern portion of their range, in western Hudson Bay, polar bears give birth between late November and early December (Derocher et al. 1992), by which time snowdrifts suitable for the construction of den sites have not yet formed in most years (Scott and Stirling 2002). In this region, it appears that bears give birth in earthen dens dug into frozen peat banks that are expanded into overlying snowdrifts later in the winter (Jonkel et al. 1972; Ramsay and Stirling 1990; Clark et al. 1997; Lunn et al. 2004). The availability of suitable denning habitat may be of particular importance to pregnant bears in western Hudson Bay, which have one of the longest fasting periods of any mammal (Ramsay and Stirling 1988). Pregnant bears may fast for up to 8 months while on land, using stored fat reserves to meet basic energetic demands as well as the increased energetic demands of gestation and lactation (Watts and Hansen 1987; Polischuk et al. 2001). In this region, pregnant bears begin to occupy dens in frozen peat banks 2–3 months in advance of parturition (Lunn et al. 2004; unpublished data), most likely as a means to escape warm ambient temperatures and conserve energy. This sort of “sheltering” behaviour has been described for polar bears elsewhere and is believed to be important during periods of cold and inclement weather and food shortage (Messier et al. 1994; Amstrup 2003).

To date, research on dens in western Hudson Bay has focused primarily on the distribution of dens, den site fidelity, structural characteristics, denning chronology, and, most recently, den disturbance (Jonkel et al. 1972; Stirling et al. 1977; Ramsay and Stirling 1990; Clark et al. 1997; Scott and Stirling 2002; Lunn et al. 2004). Despite the importance of maternity dens for population recruitment, little has been quantified about the specific habitat requirements of bears and the distribution of denning habitat in western Hudson Bay. Most of the core denning areas in the study area have been protected by the creation of Wapusk National Park. However, as the climate continues to warm, the risk of forest fires is expected to increase (Flannigan and Van Wagner 1991). Although the practice of Parks Canada is generally to allow natural processes to proceed uninterrupted, unchecked forest fires in the most important maternity denning habitat could have a significant detrimental effect on the polar bear population. Thus, the objectives of the present study were to (*i*) describe habitat characteristics of maternity den sites and document the specific resource requirements of denning female bears and (*ii*) use this knowledge to develop a resource selection function model for identifying the distribution of critical maternity denning habitat in western Hudson Bay. With this information, managers and biologists will be able to quantitatively assess the potential for the loss of critical maternity denning habitat from fire or other possible threats and determine whether preventative action is appropriate.

Materials and methods

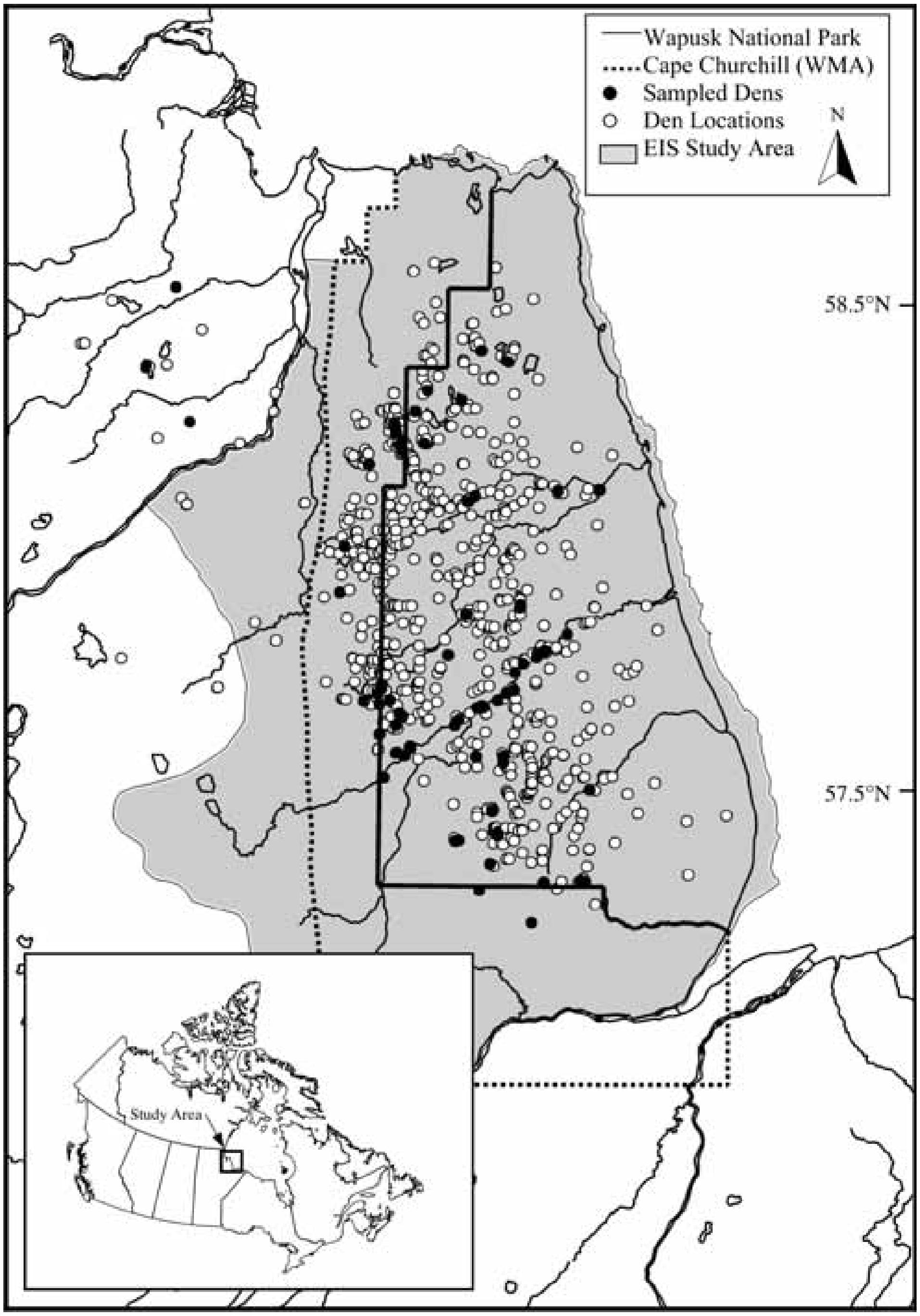
Study area

The study area covers 2200 km^2 and is located in northeastern Manitoba near Churchill, between 57°00′N and 58°50′N latitude and 92°25′W and 94°15′W longitude (Fig. 1). The area consists of an extensive peatland located in the broad transition zone between the boreal forest and the Arctic tundra (Ritchie 1960; Brook 2001). Much of the region is underlain by continuous permafrost, resulting in poor drainage and extensive bogs and fens (Brook 2001). Inland areas are characterized by open lichen tundra, with numerous lakes and small tundra ponds. Forest cover, primarily spruce (*Picea* spp.) and larch (*Larix laricina* (Du Roi) K. Koch), is most common along the edges of lakes, rivers, and streams. Coastal areas are flat and dominated by sedge meadows (*Carex* spp.), salt marshes, and interspersed relict beach ridges. Approximately 150–200 female bears produce cubs each year in the western Hudson Bay population (Derocher and Stirling 1995). Scott and Stirling (2002) estimated that more than 90% of these bears den in the study area directly southeast of Churchill, Manitoba.

Den characteristics

Den sites were located and visited nonselectively throughout the study area between mid-August and early October 2001 and 2002 while flying in a Bell 206B helicopter during surveys for polar bears, as part of a long-term population study. During these surveys, all habitats occupied by polar bears throughout the study area were surveyed at altitudes varying from 30 to 200 m above ground each year. In addition, den sites were actively searched for throughout the study area, as part of this study. The exact geographic location of each den was determined using a global positioning system (GPS). At each den site, features of relief in which dens were excavated were noted and included lake, creek, and river banks. In addition, the location of each den site was recorded as being at the top, middle, or bottom of the landform. The slope along the face of the bank at each den site was measured using an inclinometer. Bank height (metres) was measured or calculated as the side of a right triangle using the slope and the length from the top to the bottom of the feature (i.e., hypotenuse length) (see Durner et al. 2003). The aspect of each den was taken to the nearest degree using a compass. Vegetation cover and physical characteristics were also described for each den site. Vegetation composition was visually assessed as the percentage of the ground covered by each plant species in a 10 m × 10 m plot centered above the den. Plant species were further grouped by major life-form type (tree, shrub, herb, lichen, and moss), and unvegetated areas were classified as bare ground. Physical characteristics recorded included depth to permafrost, substrate stability, and substrate type. Depth to permafrost (centimetres) was measured using a steel probe with 1-cm markings at three locations for each den: (1) inside the den

Fig. 1. Map of study area showing sampled and other known polar bear (*Ursus maritimus*) den locations in northeastern Manitoba, Canada. EIS, Ecological Integrity Statement; WMA, Wildlife Management Area.



horizontally into the bank along the back wall; (2) behind the den along the top of the bank; and (3) on either side of the den along the bank. To obtain an index of substrate stability, we measured the force (kilograms) required to break the substrate surface using a four-tined garden rake attached to a 120 kg capacity scale pulled perpendicular to the substrate surface. Substrate composition was assessed based on excavated materials present at each den site and was classified as peat or sand/gravel.

A paired unexcavated comparison site was established 50 m away from each den along the same landform and was measured for the same habitat characteristics as den sites to determine whether the measured habitat characteristics were important in den site selection at a fine scale. Comparison sites were restricted to the same landform, as random selection of comparison sites would have resulted in sampling sites with different abiotic characteristics (e.g., lakes, rivers, open tundra) that are not known to support dens.

Statistical analyses

Habitat characteristics were tested for normality using Kolmogorov–Smirnov and Shapiro–Wilk tests. Characteris-

Table 1. Definition of habitat variables used for the development of denning habitat models.

Variable	Definition	Abbreviation
Larch/shrub wetland [a]	Sphagnum–larch fen; willow–birch shrub; sedge–larch fen	LSW
Sedge wetland [a]	Sedge-rich fen; sedge–bulrush poor fen; graminoid salt marsh	SW
Forest[a]	Sphagnum–spruce bog; lichen–spruce bog	FOR
Lichen tundra[a]	Lichen meltpond bog; lichen peat plateau	LTUN
Upland tundra[a]	Dry heath upland; unvegetated ridge	UTUN
Burn[a]	Recent burn; regenerating burn	BRN
Unvegetated shoreline[a]	Unvegetated shoreline	UNVEG
Water	Lakes, rivers, streams, and standing water	WATER
Normalized difference vegetation index	Measure of the proportion of photosynthetically absorbed radiation	NDVI
Greenness	Measure of reflectance of green vegetation (Crist and Cicone 1984)	GRN
Brightness	Measure of reflectance of bare soil (Crist and Cicone 1984)	BRIGHT
Wetness	Measure of soil moisture (Crist and Cicone 1984)	WET
NDVI edge	Measure of the maximum change in NDVI values between a central pixel and its neighbours in a 3 × 3 moving window	NEDG
Green edge	Measure of the maximum change in greenness values between a central pixel and its neighbours in a 3 × 3 moving window	GEDG
Distance to coast	Shortest distance to the Hudson Bay coastline from a given location	DCOAST
Distance to water	Distance to the closest pixel of water from a given location	DWATER
Distance to lichen tundra	Distance to the closest pixel of lichen tundra from a given location	DLICHEN
Distance to forest	Distance to the closest pixel of forest from a given location	DFOREST

[a]Cover types were developed from a reclassification of 16 cover types derived from a 1996 Landsat™ image of the study area (Brook 2001).

tics of den sites and comparison sites were compared using Mann–Whitney *U* tests, as the recorded habitat-characteristic data were highly skewed and could not be normalized using standard transformation techniques. The aspects of den entrances were tested for normality using Rayleigh's test for circular uniformity (Zar 1996). For data that were not uniformly distributed, a *V* test was used to determine whether the aspect data were clustered around a mean angle (Zar 1996). All tests were considered significant at $P < 0.05$. Statistical analysis and habitat modelling were performed using SPSS® version 8.0 (SPSS Inc. 1998).

Habitat modelling

Den locations were imported into ArcMap 8.1 (Environmental Systems Research Institute, Inc. 2001) and overlaid on habitat layers derived from vector- and raster-based geographic information system (GIS) files. Habitat modelling was restricted to the Ecological Integrity Statement study area for Wapusk National Park, as this represented the boundary of the available GIS layers (see Fig. 1). Cover types were derived from a habitat classification of a multispectral Landsat image (pixel size 30 m × 30 m) taken on 27 July 1996 (Brook 2001). The original accuracy assessment indicated that the image correctly classified cover types more than 88% of the time (Brook 2001). The classification included 16 cover types, which were reclassified into 7 cover types for habitat modelling (Table 1). A water layer (WATER) was derived using National Topographic System (NTS) 1 : 250 000 topographic map sheets and the water habitat class from the original habitat classification. In addition to the land-cover map, we developed several habitat covariates to describe the lichen tundra – riparian – spruce interface that was observed at most maternity den sites. These included greenness (GRN), wetness (WET), and brightness (BRIGHT) images that were produced using a tasselled cap image transformation (Crist and Ciscone 1984) from the same 1996 Landsat image used for the original habitat classification. Edge habitat between forest and upland lichen tundra (GEDG and NEDG) was identified using an edge detection algorithm in PCI (PCI Geomatics, Richmond Hill, Ontario), which assesses the maximum change in grey-level values between a central pixel and its neighbours in a 3 × 3 moving window. Proximity variables were created using a proximity algorithm in PCI that provided the proximity in pixels from a given location to the nearest pixel of a given habitat type (DWATER, DLICHEN, DFOREST). Distance to coast (DCOAST) was derived from a vector shapefile of NTS 1 : 250 000 map sheets of the Hudson Bay coastline.

A total of 1245 known den locations (Canadian Wildlife Service, unpublished data) were plotted on each of the habitat layers denoting habitat "use" in the study area. Habitat "availability" was determined by distributing 20 000 random points across the study area. Of these points, 2091 ended up being located in water; as a result, only 17 909 random points were considered "available" for our analysis. Any "used" sites that were located in water ($n = 144$) as a result of GPS error were removed from analysis. A resource selection function (RSF) was then used to determine habitat selection based on use versus availability of each habitat variable, using the following formula:

$$W^* = \exp(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_p X_p)$$

Table 2. Habitat characteristics measured at polar bear (*Ursus maritimus*) den and comparison sites in the Churchill region of Manitoba.

Den characteristic	Den site (n = 101)	Comparison site (n = 83)	P
Slope (°)	36.0±8.8 (36)	33.4±13.0 (34)	0.235
Bank height (m)	6.8±4.7 (5.77)	7.2±8.5 (5.61)	0.411
Percent tree cover	29.2±16.0 (30)	21.9±14.5 (20)	0.002
Percent shrub cover	17.9±11.2 (13)	20.2±11.6 (20)	0.094
Percent herb cover	16.7±11.5 (13)	22.5±13.5 (22)	0.002
Percent moss cover	7.4±10.3 (1)	12.3±14.2 (10)	0.034
Percent lichen cover	27.4±16.4 (30)	24.0±18.3 (30)	0.094
Percent bare ground	7.0±7.4 (10)	3.2±6.3 (0)	<0.001
Permafrost, top (cm)	35.2±17.8 (31)	28.6±12.3 (26)	<0.001
Permafrost, side (cm)	49.3±29.8 (38.5)	38.9±20.9 (31)	<0.001
Permafrost, inside (cm)	23.3±12.4 (21)	—	—
Stability, top (kg)	48.1±21.6 (46)	48.6±21.7 (45)	0.936
Stability, side (kg)	44.3±21.0 (41)	45.2±22.1 (43)	0.682
Stability, inside (kg)	12.9±9.6 (10)	—	—

Note: Values are means ± SD (median in parentheses).

where W* is an index of the probability of use of a given site (RSF) and β_1 is the selection coefficient of resource variable X_1 (Manly et al. 1993).

Model selection and validation

Univariate analysis was used to assess the significance of each habitat variable using the Wald test with a robust P value of 0.25 for inclusion in the multivariate model (Hosmer and Lemeshow 1989). All significant variables were subsequently entered into a Pearson's correlation matrix to identify collinearities between significant variables (i.e., $r_S \geq 0.7$). Variables that had collinearities were examined and the variable that explained a greater portion of the deviance was retained. All significant variables were then entered into a full model. Likelihood ratio tests (Hosmer and Lemeshow 1989) between the full model (all variables included) and reduced models (one or more variables removed) were used to assess the contribution of each remaining variable to the model. Variables were removed until the most parsimonious model was achieved, hereafter referred to as the final model. Performance of the final model was assessed using an out-of-sample k-fold cross-validation technique, where five k-fold groups were used to evaluate model adequacy. Each group consisted of a random selection of 20% of the "used" sites, which were retained for model testing; the remaining 80% of the data were used for model training (Fielding and Bell 1997; Boyce et al. 2002). To assess model performance, predicted RSF scores for the 20% of the "used sites" (withheld testing data) were placed into 10 bins using a histogram-equalized stretch technique, which assigns bins on the basis of equal frequency of occurrence (Lillesand and Kiefer 1994; Boyce et al. 2002). An area-adjusted frequency was then calculated for each bin by dividing the frequency of RSF scores within a bin by the area of that range of RSF scores available across the landscape. A high Spearman rank correlation between bin rank (i.e., 1–10) and area-adjusted frequency of cross-validated points within individual bins indicates good predictive performance of a model, as more used locations would fall within higher RSF bins (Boyce et al. 2002). We then used the coefficients from the RSF model to map the relative probability of occurrence of polar bear den sites across the study area. A linear stretch (Lillesand and Kiefer 1994) of the map was performed to scale the predicted RSF values between 0 and 1 (i.e., from least to greatest relative probability of occurrence).

Results

Den site characteristics

A total of 101 dens were sampled in the study area from September 2001 to October 2002 (Fig. 1). Dens were located between 12.6 and 80.0 km (mean ± SD = 51.5 ± 15.5 km) from the Hudson Bay coastline. Bears constructed dens primarily in riparian areas, along the edges of lakes, rivers, and creeks (n = 46, 47, and 8, respectively). Within riparian areas, dens were located primarily at the top of banks (n = 80), although some dens were located in the middle (n = 16) and, to a lesser degree, at the bottom (n = 5). Bank height and slope at den sites did not differ significantly from those at comparison sites (P = 0.411 and P = 0.235, respectively; Table 2). Aspects of den sites were significantly different from a random distribution (Z = 3.47, U = 2.63, P < 0.005), with a mean azimuth of 123°.

Vegetation cover at den sites consisted primarily of tree cover, which was significantly greater than at comparison sites (29.2% ± 16.0% and 21.9% ± 14.5%, respectively; Table 2). Den sites and comparison sites had similar amounts of lichen and shrub cover (P = 0.094 and P = 0.094, respectively; Table 2). However, percent herb cover and percent moss cover at den sites were significantly less than at comparison sites (P = 0.002 and P = 0.034, respectively; Table 2). Den sites had significantly more bare ground than comparison sites (7.0% ± 7.4% and 3.2% ± 6.3%, respectively, P < 0.001).

Depth to permafrost at dens was greatest along the sides of banks (49.3 ± 29.8 cm), slightly less behind dens along the top of banks (35.2 ± 17.8 cm), and the least inside dens (23.3 ± 12.4 cm). Comparison sites had similar values of 28.6 ± 12.3 cm and 38.9 ± 20.9 cm for the top and sides of banks, respectively (Table 2). Depth to permafrost was significantly greater at den sites than at comparison sites along

Table 3. Variables in multiple logistic regression analysis of the final denning habitat model showing coefficients, standard errors, *t* ratios, and significance values from the Wald test.

Variable	Coefficient	SE	*t* ratio	*P*
NDVI	3.093	0.368	25.870	<0.001
BRIGHT	0.006	0.002	11.637	0.002
NEDG	15.642	0.606	12.372	<0.001
DWATER	–0.212	0.017	3.358	<0.001
DLICHEN	–0.161	0.014	3.176	<0.001
DFOREST	–0.101	0.032	9.831	<0.001

Note: Variable abbreviations are defined in Table 1.

Table 4. *K*-fold cross-validated Spearman rank correlations between RSF bin ranks and area-adjusted frequencies for the average and individual test sets.

Test set	Spearman rank correlation	*P*
1	1.00	0.01
2	0.976	<0.001
3	1.00	0.01
4	1.00	<0.001
5	1.00	<0.001
Average	0.99	

both the top and the sides of banks ($P < 0.001$ for both; Table 2).

Mean substrate stability on top of dens was not significantly different from that at comparison sites (48.1 ± 21.6 kg and 48.6 ± 21.7 kg, respectively, $P = 0.936$). Substrate stability on the sides of dens was less than that at comparison sites (44.3 ± 21.0 kg and 45.2 ± 22.1 kg, respectively), although this difference was not significant ($P = 0.682$). However, within den sites, substrate stability at the top and sides of dens was significantly greater than that inside dens (12.9 ± 9.6 kg) ($P < 0.001$ and $P < 0.001$, respectively). Bears showed little variation in selection of different substrate types and denned almost exclusively in peat substrates ($n = 100$), with the exception of one den excavated in sand/gravel.

Denning habitat model

Initial univariate analysis indicated that 13 of the 18 habitat variables contributed significantly to the response variable. Collinearities existed between GRN and NDVI as well as between GRNEDG and NEDG. Because NDVI and NEDG explained a greater portion of the deviance, GRN and GRNEDG were removed from further analysis. Likelihood ratio tests on reduced models were used to assess the significance of individual variables. Reduced models with the variables SW, LSW, and BRN removed were as good as the full model at predicting used locations (likelihood ratio [2(LL full model – LL reduced model)] = 2.746, df = 3, $P = 0.433$). LTUN contributed significantly to the prediction of the response variable; however, the negative selection coefficient for LTUN contrasted with the close association of den sites with lichen tundra observed during site-level analysis, so the variable was removed. Coefficients and significance values for variables in the final model are shown in Table 3. Den occurrence was positively associated with NDVI, NEDG, and BRIGHT, and negatively associated with increasing DWATER, DTLICHEN, and DFOREST, which indicated selection for sites in riparian areas in close proximity to lichen and forest. Spearman rank correlations between RSF bins and area-adjusted frequencies were extremely high, indicating good predictive performance of the model (Table 4). Using selection coefficients from our model, we developed a denning habitat map predicting the relative probability of occurrence of polar bear maternity den sites in the study area (Fig. 2).

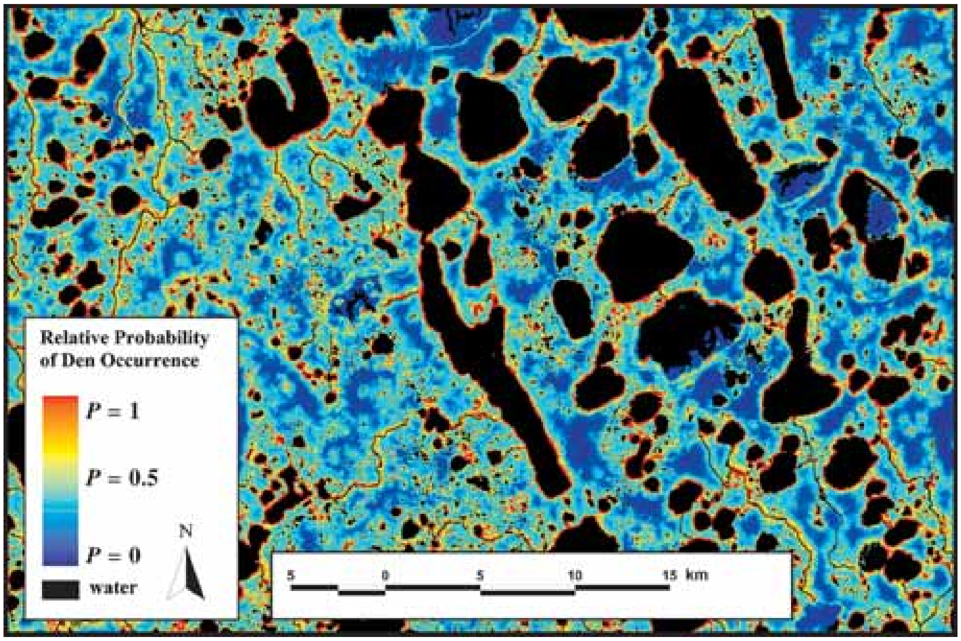
Discussion

This is the first study to examine the specific resource requirements of female polar bears making use of earthen maternity den sites. Results indicated that female bears preferentially established den sites in areas with certain habitat characteristics. At the landform scale, bears denned almost exclusively within frozen peat banks in riparian areas (lakes, rivers, and creeks) that provided sufficient relief for the construction of dens. In Alaska, Durner et al. (2001) described dens dug in snow in association with similar landscape features including coastal banks, river banks, floodplain banks, tributaries, and lake shores, where wind-blown snow accumulates in the winter. Similarly, grizzly bears (*Ursus arctos* L., 1758), the closest relatives of the polar bear (Kurtén 1964), are known to use earth dens along the banks of lakes, creeks, and river channels in tundra habitat on Richards Island, Northwest Territories (Harding 1976; Nagy et al. 1983*b*). Harding (1976) suggested that grizzlies may exhibit a preference for bank habitat because of the ease of digging on a horizontal plane as well as the potential to dig on an upward-sloping plane, which helps to exclude snow and creates a warm-air trap, a feature that is often characteristic of snow dens excavated by polar bears (Harington 1968).

It is likely that polar bears in western Hudson Bay den in peat banks for similar reasons. Bears in the study area preferentially excavated dens at the top of banks, similar to dens located in sand ridges on the islands of James Bay (Doutt 1967). Conversely, Jonkel et al. (1972) noted that bears on the Twin Islands in James Bay constructed dens in the middle or lower portions of slopes and extended them higher each year as the overhang collapsed. We suggest that bears may show a preference for dens located at the top of banks in the study area because (*i*) they may provide certain microhabitat characteristics favourable for denning, including a spruce root matrix that provides stability to the roof of the den site, preventing the overhang from collapsing, and (*ii*) the height of most banks is limited to a few metres or less, so dens need to be located at the top of banks simply to be above the water table in riparian areas, providing a drier environment for denning.

Bears selected den sites in areas of moderate slope similar to that of snow dens occupied by bears in other areas. In Alaska, slopes at polar bear dens range from 8° to 50° (Durner et al. 2001, 2003). Harding (1976) reported that slopes at most grizzly bear dens on Richards Island ranged between 30° and 50°. Similarly, Pearson (1975) noted that grizzly bears in the Yukon usually denned in slopes of 30°–40°. Nagy et al. (1983*b*) reported a mean slope of 32.7° at

Fig. 2. Predicted relative probability of polar bear (*U. maritimus*) maternity den sites in northeastern Manitoba. Warmer colours represent higher resource selection values and increased relative probabilities of den occurrence.



grizzly bear den sites on the Tuktoyuktuk Peninsula and Richards Island in the Northwest Territories. The consistency of slopes at grizzly and polar bear den sites is likely the result of a trade-off between the stability of level ground and the ease of digging at sites with steeper slopes. Furthermore, the absence of earth dens on level ground in this study is consistent with early research conducted in the study area by Jonkel et al. (1972), potentially indicating the importance of slope in den site selection.

In addition to slope, bank height also appears to be an important factor determining den site selection. Bank heights reported by Durner et al. (2003) and Durner et al. (2001) ranged between 1.4 and 33 m and between 1.3 and 34 m, respectively, and are similar to those reported here. However, of greater significance is the consistency of the minimum bank heights in which dens were dug, which likely represents the minimal relief required for den structures (i.e., den tunnels and chambers). Clark et al. (1997) reported an average (±SD) chamber height of 90 ± 13 cm for recently used peat dens in our study area, which is consistent with the internal dimensions reported for snow dens elsewhere. In the Canadian Arctic, Harington (1968) reported a mean chamber height of 97 cm. Lentfer and Hensel (1980) reported a mean chamber height of 78 cm for snow dens in Alaska. Den chamber heights on Wrangel Island were 80 cm (Uspenski and Kistchinski 1972), while Larsen (1985) noted a range in chamber heights from 70 to 130 cm. Taken together, these values suggest that an approximate minimum of 1.0 m of relief is likely required for the construction of a maternity den. However, because the average bank height at den sites in the study area was 6.8 ± 4.7 m, it appears that female bears prefer more well-developed peat banks for denning.

Jonkel et al. (1972), Ramsay and Stirling (1990), and Clark et al. (1997) all noted that maternity dens in the study area most commonly have southerly aspects. In this study, the distribution of den azimuths was clustered around a mean azimuth of 122.5°, which is oriented away from the prevailing northwest winds. Harington (1968), Harding (1976), and Larsen (1985) all reported that polar and grizzly bear dens were located primarily on leeward slopes and suggested that there was a preference for these sites due to increased accumulation of snow. Snow accumulation on leeward slopes may be further enhanced by the presence of vegetation at or above den sites (Pearson 1975; Nagy et al. 1983*b*; Scott and Stirling 2002), which would provide insulation for denning bears and a more favourable microenvironment for developing young. Alternatively, several observers have suggested that a southerly entrance orientation at arctic fox (*Alopex lagopus* (L., 1758)) dens may provide microclimatic advantages (Chesemore 1969; Prestrud 1992; Smits and Slough 1993); if so, such an orientation could provide similar thermoregulatory advantages for denning female polar bears. In addition, slopes with southerly aspects receive more solar radiation, potentially increasing permafrost thaw and the ease with which dens are excavated. Field observations of claw marks in the permafrost inside dens indicate that bears have only limited success in excavating frozen peat.

Several authors have suggested that the presence of roots from vegetation may help stabilize the ceilings of terrestrial dens dug by bears and wolves (Craighead and Craighead 1972; Jonkel et al. 1972; Pearson 1975; Harding 1976; Nagy et al. 1983*a*, 1983*b*; Heard and Williams 1992; Norris et al. 2002). However, this hypothesis has never been quantitatively assessed. Substrate stability measurements in the root matrix at the top of dens in this study indicated that the presence of trees and other vegetation plays an important role in stabilizing terrestrial den sites. Comparisons between substrate stability inside dens (i.e., unvegetated) and that outside dens (along the sides and top of banks) indicate that vegetation may increase substrate stability as much as fourfold, thus stabilizing the ceilings of terrestrial dens. Although roots from vegetation provide a significant degree of stability to den sites, the fibrous nature of peat substrates likely provides a greater degree of stability than that of particulate substrates such as gravel and sand, which have limited cohesion between soil or rock particles. Dens excavated by polar bears in sand may start to collapse after only a few weeks (Doutt 1967), thus making dens in sand unsuitable for long-term use. Although extensive gravel and sand banks exist in our study area (e.g., along the banks of the Owl and Broad rivers) and are used for denning in southern Hudson Bay (Doutt 1967; Jonkel et al. 1976), bears in the study area denned almost exclusively in frozen peat banks. In addition to the stability of peat substrates, preliminary data from temperature recordings inside peat dens and an artificial den dug in gravel and sand indicate that dens in peat remain several degrees warmer during the winter than those in gravel and sand (I. Stirling, unpublished data). Although the southern Hudson Bay polar bear population is the only other polar bear population known to use peat dens, use of peat dens by grizzly bears has been described by Nagy et al. (1983*a*, 1983*b*). We suggest that the preference for denning in peat observed here likely results from a combination of peat being easier to dig in than gravel and the superior structural and insulative qualities of peat. Although peat may be removed with relative ease (personal observations), the persistence of permafrost throughout the year may limit the extent to which a bear can excavate a den in a single attempt. Harding (1976) suggested that the ease of digging in exposed and thawed or partially thawed soils might also contribute to the advantages of denning in banks. Permafrost measurements taken directly from the sides of banks in this study support the hypothesis that a deeper active layer along the sides of banks may make them more attractive for digging. The active layer was the shallowest inside dens, possibly as a result of the cooler microclimate (Clark et al. 1997) and the excavation of the active layer by bears in recently used dens. In addition to providing a cool microclimate inside dens, the persistence of permafrost in peat banks also provides a significant degree of substrate stability. Observations made in burned areas indicate that permafrost degradation as a result of fire can result in extensive slumping of peat banks and the collapse of earth dens (Richardson 2004). Current climatic models indicate that the Hudson Bay region is at risk of permafrost degradation as a result of climate change, with the potential for a substantial reduction of permafrost in the next 50 years (Gough and Leung 2002). The cumulative effects of habitat loss as a result of fire and regional-scale permafrost degradation have the potential to significantly reduce the availability of polar bear maternity denning habitat in western Hudson Bay.

Throughout most of their range, polar bears den relatively close to the coast, with the exception of those in Hudson Bay, which travel between 7 and 150 km inland to denning areas (Stirling et al. 1977; Kolenosky and Prevett 1983). In Alaska, Durner et al. (2003) reported a mean distance from the coast of 1.7 ± 4.5 km with a range of 0–24.7 km. The mean distance to the coast of den sites on the Simpson Peninsula was 5.5 ± 9.4 km for female bears (Van de Velde et al. 2003). In the Northwest Territories, Harington (1968) reported that 61% (n = 69) of dens were within 8 km of the coast. Messier et al. (1994) reported an average (±SE) distance of 8.6 ± 1.5 km for polar bear maternity den sites in the Viscount Melville Sound in the Canadian Arctic. Van de Velde et al. (2003) suggested that selection of den sites may be influenced by the distribution of adult males, the availability of suitable snowdrifts, and a preference for travelling no farther than necessary in the spring to return to the sea ice to hunt seals. We suggest that the primary reason that bears in western Hudson Bay do not den close to the coast is a lack of suitable peat banks in coastal areas in comparison to the well-developed, thicker peat banks that are found farther inland. In other portions of the polar bear range, the availability of sufficient snowdrifts determines the distribution of maternity dens (Belikov 1980; Lentfer and Hensel 1980; Hansson and Thomassen 1983; Durner et al. 2003). Similarly, it appears that the availability of suitable denning habitat (i.e., peat banks) determines the distribution of dens in western Hudson Bay.

Because denning is necessary for polar bear reproduction, identification and protection of maternity denning habitat is crucial. However, accurate and predictable identification of denning habitat in most areas, with the exception of coastal Alaska (Durner et al. 2001), has been limited by the spatial and temporal variability of snowdrifts in which most bears den. To assess the relative probability of occurrence of den sites on the landscape, we developed an RSF model using remote sensing imagery and GIS. RSF models often make use of what has been referred to as a top-down approach to habitat modelling in which GIS and remote sensing data, along with radiotelemetry locations and habitat modelling, are used to describe the relative probability of occurrence of a given species (Nielsen et al. 2003). A potential limitation of this approach is that it does not provide causal insights into the habitat selection process, bringing into question the biological meaning of the explanatory variables (i.e., habitat covariates) in these models (Lennon 1999; Nielsen et al. 2003). To gain insight into the selection of polar bear maternity den sites, we adopted a bottom-up approach to the development of our RSF model: we first described the specific resource requirements of denning female bears and then developed several habitat covariates for the model based on this knowledge.

Our model indicated a positive association between dens and areas in close proximity to water, which served as a proxy to help identify peat banks along lakes, rivers, and creeks that were selected for at the den-site level. Bears also used areas for denning that were in close proximity to lichens and positively associated with brightness values. Observations of lichen-dominated areas behind dens indicated that these sites were well drained and often contained day beds that were used by bears. The importance of tree cover and vegetation along banks was evident from the positive association of used sites with NEDG and high NDVI values. Collectively, all these variables effectively described the lichen tundra – riparian – spruce interface that was selected for at the site level.

The RSF model performed well in predicting sites used by bears, with a mean Spearman rank correlation of 0.99 (P < 0.001) (Table 4). The high correlations observed between RSF bins and area-adjusted frequencies may be a result of the very large portions of the study area that had relatively low RSF values in relation to the sample sizes of cross-validation groups. A potential limitation of the k-fold cross-validation technique is that false positives (i.e., high RSF values in low-quality habitat) are not detected. We recognize this potential limitation; however, given the performance of the model and the fact that false positives would result in increased habitat protection, we suggest that our model is conservative in its protection of polar bear maternity denning habitat. Although the denning model performed well in predicting used sites, the importance of site-level characteristics (i.e., bank height, slope, and aspect) in den site selection must also be considered when determining the suitability of denning habitat. Unfortunately, detailed topographical data for our study area are not available and thus could not be included in our denning habitat model. The distribution of denning habitat identified by the denning model across the study area showed a high degree of spatial overlap with the previously recorded distribution of den sites throughout the Churchill region, providing further support to the predictive ability of the model. Although den location (i.e., used sites) data were collected over the past three decades, we suggest that the denning map likely represents a much more long-term pattern of den site selection in this population, as dens are persistent features on the landscape and may be used periodically for periods that may exceed a century (Scott and Stirling 2002).

Understanding the link between species resource requirements and landscape composition is an important step toward providing insight into the habitat selection process (Boyce and McDonald 1999; Fernández et al. 2003; Nielsen et al. 2003). In this study, the development of a denning model based on a detailed analysis of polar bear maternity den sites has provided insight into the mechanistic links between selected variables in the denning habitat model and the specific resource requirements of denning bears. Knowledge of the distribution of denning habitat is necessary to avoid potential impacts of anthropogenic disturbance and to assess the potential impacts of habitat loss due to forest fires (Richardson 2004). Ultimately, this information will allow resource managers to develop effective management strategies for the conservation of polar bear maternity denning habitat in western Hudson Bay.

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