

Habitat selection and spatial relationships of black bears (*Ursus americanus*) with woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberta

A.D.M. Latham, M.C. Latham, and M.S. Boyce

Abstract: Populations of woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) have declined across much of their range. Wolves (*Canis lupus* L., 1758) are believed to be responsible for the majority of mortality in adult female caribou; however, we hypothesize that other predators such as black bears (*Ursus americanus* Pallas, 1780) may be important contributors to calf mortality. We assessed habitat selection by black bears and spatial relationships of caribou – black bears during the caribou calving season in northeastern Alberta, Canada. Black bears avoided bogs and fens, while selecting upland mixed woods and various industrial features. Conversely, caribou showed strong selection for bogs and fens relative to bears, supporting the hypothesis that caribou in the boreal forest attempt to minimize predation risk by selecting peatlands to avoid areas frequented by predators. However, habitat selection by individual black bears was highly variable and some bears selected habitats similar to those selected by caribou, i.e., bogs and fens. Bears that specialize on foraging in peatlands might be responsible for some of the predation on caribou calves. Because declines in caribou populations have resulted from a combination of high adult female and calf mortalities, management actions to conserve woodland caribou should consider the entire suite of potential predators rather than focusing only on wolves.

Résumé : Les populations de caribous des bois (*Rangifer tarandus caribou* (Gmelin, 1788)) affichent un déclin sur une grande partie de leur aire. On croit que les loups (*Canis lupus* L., 1758) sont responsables de la majeure partie de la mortalité des caribous femelles adultes; nous émettons, néanmoins, l'hypothèse selon laquelle d'autres prédateurs, tels que les ours noirs (*Ursus americanus* Pallas, 1780), peuvent contribuer de façon importante à la mortalité des petits. Nous avons évalué la sélection d'habitat chez l'ours noir et les relations spatiales caribous–ours noirs durant la saison de mise bas des caribous dans le nord-est de l'Alberta, Canada. Les ours noirs évitent les tourbières hautes et basses, mais choisissent les boisés mixtes des terres hautes ainsi que diverses installations industrielles. À l'inverse, les caribous montrent une forte sélection pour les tourbières hautes et basses par comparaison aux ours, ce qui appuie l'hypothèse qui veut que les caribous dans la forêt boréale essaient de minimiser leur risque de prédation en choisissant des milieux tourbeux afin d'éviter les régions fréquentées par les prédateurs. Cependant, la sélection d'habitat par les ours noirs individuels est très variable et certains ours choisissent des habitats semblables à ceux sélectionnés par les caribous, c'est-à-dire des tourbières hautes et basses. Les ours qui recherchent leur nourriture dans les milieux tourbeux pourraient être responsables d'une partie de la prédation sur les petits des caribous. Parce les déclin des caribous ont été causés par une combinaison de fortes mortalités chez les femelles adultes et les petits, les opérations de gestion pour la conservation des caribous des bois devraient tenir compte de l'ensemble complet des prédateurs potentiels plutôt que se concentrer seulement sur les loups.

[Traduit par la Rédaction]

Introduction

Predation is a limiting factor in many ungulate populations (Keith 1974; Messier 1994; Bergerud and Elliott 1998). In North America, declines of some ungulate populations have been attributed to predation by wolves (*Canis lupus* L.,

1758) (Bergerud and Elliot 1986); however, other predator species also can contribute to ungulate mortality (Truett et al. 1989; Ballard 1994). Prior to the use of radiotelemetry, grizzly bears (*Ursus arctos* L., 1758) and black bears (*Ursus americanus* Pallas, 1780) were thought to be primarily scavengers of ungulates (Jonkel 1978). However, grizzly bears are

Received 6 August 2010. Accepted 22 December 2010. Published at www.nrcresearchpress.com/cjz on 12 April 2011.

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now known to be effective predators of calves of moose (*Alces alces* (L., 1758)) and caribou (*Rangifer tarandus* (L., 1758)) (Ballard et al. 1981, 1990; Bergerud and Page 1987; Whitten et al. 1992; Young and McCabe 1997), whereas black bears have been identified as effective predators of calves of caribou (Mahoney et al. 1990; Seip 1991; Ballard 1994), elk (*Cervus elaphus* L., 1758) (Schlegel 1976), and moose (Franzmann et al. 1980; Nolan and Barrett 1985), as well as fawns of white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) and mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) (Wilton 1983; Kunkel and Mech 1994). Bear predation on ungulate neonates is most likely to occur during the first 4–6 weeks of life (Bergerud 1971; Ballard et al. 1981), with neonate vulnerability decreasing as age and mobility increase (Ballard et al. 1980; Truett et al. 1989).

Boreal populations of woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) in Alberta, Canada, have shown gradual declines over the past 60 years (Edmonds 1988; Dzus 2001), with some herds declining significantly in the past 10 years (McLoughlin et al. 2003; Latham et al. 2011). Caribou in Alberta are formally listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002) and under the federal Species at Risk Act (SARA) (Environment Canada 2008). Although a number of factors have been implicated in these declines, predation is considered to be the major mortality factor for woodland caribou in Alberta (Fuller and Keith 1981; Dzus 2001; McLoughlin et al. 2003). However, because caribou have coexisted with predators in the boreal forest for thousands of years and yet only recently face extirpation from much of their range (McLoughlin et al. 2003), it has been hypothesized that recent intensive industrial activity might have altered caribou–predator relationships (James et al. 2004). For example, numbers of white-tailed deer have increased in northeastern Alberta in the last decade, likely because forest harvesting has increased suitable deer habitat; a factor that has resulted in a numeric response by wolves (Latham et al. 2011). Wolves are believed to be responsible for the majority of mortality in adult female caribou (Dzus 2001; McLoughlin et al. 2003). However, population declines are believed to have occurred not only because of low adult female survival, but also because of low calf survival and subsequent low recruitment (Dzus 2001). Although wolf predation likely contributes to low caribou calf survival, grizzly bears, black bears, coyotes (*Canis latrans* Say, 1823), Canada lynx (*Lynx canadensis* Kerr, 1792), and wolverine (*Gulo gulo* (L., 1758)) also may be important predators of calves (Mahoney et al. 1990; Stephenson et al. 1991; Ballard 1994; Crête and Desrosiers 1995; Rettie 1998; Dzus 2001).

Alberta has approximately 40 000 black bears (Gunson 1993) found throughout ranges of boreal ecotype woodland caribou in northern and northeastern Alberta (Dzus 2001). Ballard (1992) found that black bears were a significant source of mortality to moose calves where densities exceeded 200 black bears/1000 km², and Wilton (1983) states that black bears should be considered effective predators of ungulates throughout their range. In northeastern Alberta, densities of 370 black bears/1000 km² have been reported (Young and Ruff 1982); in contrast, wolf densities are comparatively low (11.5 wolves/1000 km²; Latham 2009; Latham et al. 2011). Similarly, bear densities are almost an order of

magnitude higher than caribou densities (the 1990s estimate was approximately 41 caribou/1000 km²; Stuart-Smith et al. 1997). Accordingly, black bears have the potential to constitute a large source of mortality for the boreal ecotype of woodland caribou throughout much of the province.

To date little information exists on habitat use of black bears in caribou ranges in Alberta. The aim of this study was to assess habitat selection by black bears and spatial relationships of caribou – black bears during the caribou calving season (late-April to 30 June) in a caribou range in northeastern Alberta from 2000 to 2004. We used three methods to assess this objective. First, we assessed patterns of habitat selection by black bears at the population level. However, we suspected that a population-level model of habitat selection by black bears might only provide us with general patterns of selection (Boyce et al. 2003), supporting the well-known generalist nature of these animals (Young and Ruff 1982; Czetwertynski 2007; Garshelis 2009), and potentially masking any impact that individual black bears might be having on caribou. Consequently, as a second step we further analyzed habitat selection of black bears by assessing individual bear selection for caribou-preferred habitats (i.e., bogs and fens). Finally, we hypothesized that if black bears are an important mortality factor for caribou calves, we would expect to find a high level of spatial overlap with caribou during the calving period. To assess this, we analyzed the relative strength of selection for habitat types available in the study area by black bears compared with caribou during the calving season.

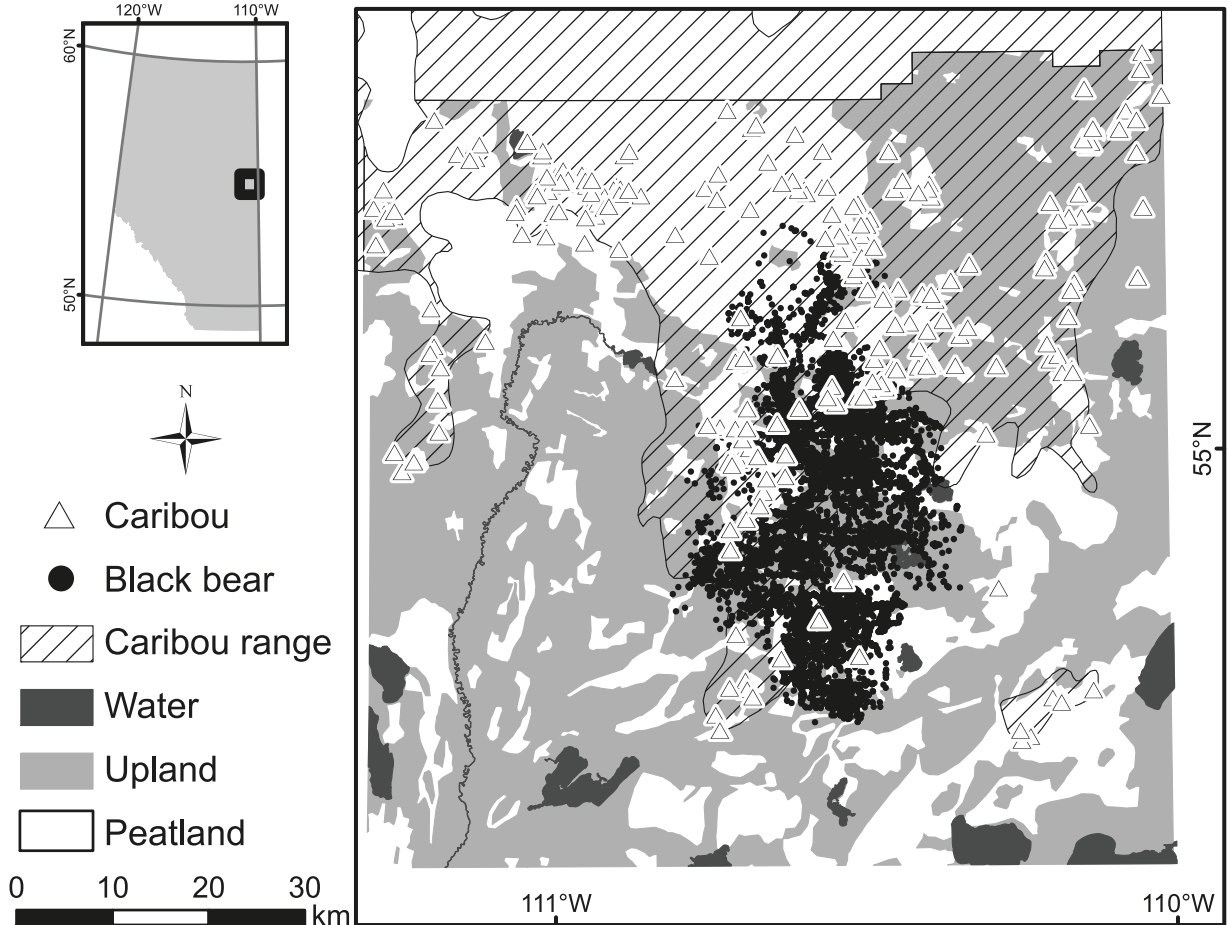
Materials and methods

Study area

We assessed spatial relationships of black bears – caribou in the Cold Lake Air Weapons Range (CLAWR) in northeastern Alberta (Fig. 1). CLAWR is located to the north of the town of Cold Lake (54°24'N, 110°12'W). The range straddles northeastern Alberta and northwestern Saskatchewan and covers approximately 11 600 km². Our study was confined to the Alberta portion of CLAWR (5100 km²) and areas immediately adjacent to the range in Alberta (all of which hereafter we refer to as CLAWR). Access restrictions to civilians were enforced within the range boundaries, but there were no access restrictions outside of the range. Similarly, hunting was permitted outside of the range, but with the exception of restricted access for Cold Lake First Nations (CLFN), hunting was not permitted on the range (Czetwertynski 2007). Moose were the primary species of interest for CLFN hunters, both on the range and on the adjacent land (Czetwertynski 2007).

Our study area was typified by rolling mixed-wood boreal forest and peatlands that were interspersed with lightning-caused burned areas. Upland mixed woods were dominated by quaking aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) P. Mill.), and jack pine (*Pinus banksiana* Lamb.). Peatlands were dominated by bogs of black spruce (*Picea mariana* (P. Mill.) B.S.P.) and fens of black spruce – tamarack (*Larix laricina* (Du Roi) K. Koch). Labrador tea (*Ledum groenlandicum* Oeder), bog birch (*Betula pumila* L.), willows (genus *Salix* L.), sedges (genus *Carex* L.), peat moss

Fig. 1. The study area in the Cold Lake Air Weapons Range in northeastern Alberta, Canada. The town of Cold Lake is located directly to the south of the range (54°24'N, 110°12'W). Within this area, we radio-collared 15 black bears (*Ursus americanus*) and 37 adult female woodland caribou (*Rangifer tarandus caribou*) between 2001–2003 and 2000–2004, respectively.



(genus *Sphagnum* L.), and a variety of terrestrial lichens dominated ground cover in peatlands. There is minimal topographic relief in the study area, with elevation varying from 600 to 800 m above sea level. Numerous small rivers and streams occurred throughout the region.

Oil and gas extraction was prominent on the Alberta portion of CLAWR, as well as areas adjacent to the range. Energy-sector activity consisted of the creation of seismic lines (2–8 m wide) for exploration purposes and the creation of well pads (1 ha), pipelines, and roads for extraction purposes. A 42 km all-season road provided the main north-south connection to the majority of oil and gas extraction activities in CLAWR (Czetwertynski 2007). In addition, there were access roads to well pads that were typically oriented east-west and occurred at 1–2 km intervals. Five energy-sector camps were located along the main road in CLAWR and all were surrounded by electrified fencing to reduce human-bear conflicts (Czetwertynski 2007). Timber harvesting occurred outside of CLAWR, but did not occur on the range. Because of the lack of merchantable timber in peatlands, harvesting was confined primarily to upland forest.

Animal capture and radio-collaring

Black bears were captured between 2001 and 2003 using modified bucket traps (Lemieux and Czetwertynski 2006)

and L-83 ground snares (Jolicoeur and Lemieux 1992). Once restrained, bears were immobilized with tiletamine-zolazepam (University of Alberta Animal Care Protocol No. 322104) and a subset of captured bears was equipped with global positioning system (GPS) 2200L radio collars (Lotek Wireless Inc., Newmarket, Ontario, Canada). Access permits within the CLAWR allowed trapping within 1 km of roads (Czetwertynski 2007); access was farther restricted by peatlands scattered throughout the study area (Czetwertynski 2007). GPS radio collars were programmed to record hourly fixes. If individuals were monitored for more than 1 year, data from separate years were merged and all locations were assigned to that bear.

Telemetry data of caribou were obtained from 37 very high frequency (VHF) radio-collared (Lotek Wireless Inc., Newmarket, Ontario, Canada) adult female caribou in the CLAWR range collected between 2000 and 2004. Caribou were captured in winter using a helicopter and net-gun (McLoughlin et al. 2003). Caribou were relocated weekly during the calving season.

Landscape covariates

Explanatory landscape variables were derived from a geographic information system (GIS) of the study area using ArcGIS version 9.3 (ESRI 2008) and included the following:

cover type; distance to nearest human habitation (i.e., oil and gas camps — there were no hamlets or towns in the study area); distance to nearest seismic line; distance to nearest road; distance to nearest pipeline; distance to nearest linear feature (seismic lines, roads, and pipelines combined); distance to nearest river or stream; distance to nearest perennial lake; distance to nearest oil and gas well; distance to upland habitat edge (a greater distance from upland habitat edge reflects more suitable caribou habitat); proportion of oil and gas wells; and linear feature density (see Table 1). We defined “landscape feature” as any explanatory variable, whereas cover type was used to define forested and nonforested cover classes.

Cover type was obtained from the Alberta Ground Cover Classification (AGCC) (Young et al. 2006). The AGCC is a classified mosaic of Landsat 7 TM (25 m × 25 m pixels) satellite images completed for Alberta with the aim of providing landscape cover information ca. 2000 for the province. The AGCC was reclassified into five forest cover classes (bog, deciduous, fen, mixed wood, and upland conifer, occupying 12%, 16%, 9%, 6%, and 49% of the study area, respectively) and 1 nonforested cover class (water). In addition, we reclassified the AGCC into three additional cover classes: anthropogenic (including oil and gas camps and major roads, but excluding forestry cutblocks), lightning-caused burns, and open habitat (including forestry cutblocks and agriculture). Discrete landscape cover types were converted to the proportion of each class within a 500 m radius circular buffer around each bear or caribou GPS or VHF telemetry location.

Distance to covariates were calculated as the shortest distance between each bear or caribou location and the nearest landscape feature and were measured in kilometres. To quantify distance to upland habitat edge, we identified upland habitat from the Peatland Inventory of Alberta (Vitt et al. 1998). Point locations for oil and gas wells were converted into 1 ha square polygons (representing the well pad) and the proportional area of wells within a 500 m radius circular buffer around each location of black bear was calculated. Linear feature density included all anthropogenic linear features (i.e., seismic lines, roads, pipeline right of ways, power lines, and winter access ways), and was calculated as edge density (length/area) within a 500 m radius circular buffer around each bear or caribou location. We screened against including collinear variables using a $|r| = 0.7$ as a threshold cut-off value (Tabachnick and Fidell 1996; Hosmer and Lemeshow 2000).

Population-level habitat selection by black bears

We assessed patterns of habitat selection by black bears at the population level during the caribou calving season (late-April to 30 June) using GPS locations from 15 black bears captured within the CLAWR. Because we were interested in those biophysical factors that were associated with foraging by black bears, we excluded GPS locations associated with known den sites (Czetwertynski 2007). To do this, we visually identified the cluster of GPS points representing the den site for each individual bear occurring from 11 April (earliest available date) to 15 May. We applied a 50 m radius circular buffer around each den and removed any locations that fell within that area, i.e., we made the assumption that because those locations were associated with resting, the bears were

not hunting or foraging when inside the buffer. A 50 m radius circular buffer was used because it was the smallest area that encompassed the cluster of locations associated with the identified den site. The mean number of locations excluded from den sites per GPS-collared bear was 64 (range = 0–285; $n = 15$ bears). Furthermore, we randomly selected eight locations per bear daily (i.e., 24 h cycle) to reduce the potential for spatial autocorrelation resulting from using successive locations separated by 1 h.

Based on the used-versus-available method, we estimated resource selection functions (RSF) by comparing landscape features at bear GPS locations (used) and random (available) locations using logistic regression (Manly et al. 2002; Johnson et al. 2006). We used generalized linear mixed models (GLMM) to account for individual-level heterogeneity in resource selection by including a random intercept for each of the 15 bears (Skronald and Rabe-Hesketh 2004; Gillies et al. 2006; Hebblewhite and Merrill 2008). Because we were constrained to capture black bears within 1 km of roads, the collection of GPS locations of black bears that we obtained was not evenly distributed across the CLAWR (Fig. 1). Consequently, to avoid including areas for which we did not have information for bears, we constrained the domain of availability to the 100% minimum convex polygon (MCP) encompassing all of the calving-season bear locations (i.e., second-order selection, Johnson 1980; also see Boyce 2006), and drew random locations from this area using a 1:1 ratio of used to available locations (which equated to 8 random points/km² of bear territory).

Information-theoretic methods were used for model selection from a set of a priori candidate models (Burnham and Anderson 2002) based on knowledge of the ecology of black bears. These included five alternative models, each depicting a different combination of variables thought to influence habitat selection by black bears during the caribou calving season (Table 2). We created a model similar to Czetwertynski (2007) that included covariates for conifer and deciduous forests, distance to nearest road, well, and water source, as well as distance to nearest linear feature. We also created a model containing only anthropogenic covariates and another model using solely natural habitat covariates. To test the hypothesis that at the population level black bears are selecting the same habitat types as caribou (and could be a potential source of mortality for caribou calves), we created a model to reflect habitats that caribou have been previously shown to select (Bradshaw et al. 1995; Stuart-Smith et al. 1997; Dzus 2001). Finally, we created a global model including all of the predictor covariates. DLFk and DWellk from the Czetwertynski model were correlated with DSeisk ($r = 0.689$) and Well ($r = -0.883$), respectively, and thus were not included in the global model (Table 2).

We verified the assumption of linearity between the relative selection of the response and each candidate covariate using smoothed scatterplots (Hosmer and Lemeshow 2000). Akaike's information criterion (AIC) was used to rank candidate models (Boyce et al. 2002; Burnham and Anderson 2002). We used k -fold cross-validation to evaluate model performance (Boyce et al. 2002).

Habitat selection by individual black bears

We suspected that a population-level model of habitat se-

Table 1. Explanatory variables used in the analyses of black bears (*Ursus americanus*) and woodland caribou (*Rangifer tarandus caribou*) during the caribou calving season in the Cold Lake Air Weapons Range, northeastern Alberta, Canada, 2000–2004.

Variable	Description	Minimum	Maximum	Mean	SD
DRivk	Distance to nearest river or stream (km)	0	3.377	0.743	0.608
DPerlak	Distance to nearest perennial lake (km)	0	5.746	1.839	1.171
DSeisk	Distance to nearest seismic line (km)	0	2.899	0.400	0.348
DRoadk	Distance to nearest road (km)	0	14.978	4.357	3.519
DPipek	Distance to nearest pipeline (km)	0	6.777	0.835	0.933
DLFk	Distance to nearest linear feature (km)	0	2.143	0.265	0.265
DUrbank	Distance to nearest human habitation (km)	0	18.468	3.691	4.008
DWellk	Distance to nearest oil and gas well (km)	0	3.205	0.627	0.461
DUplk	Distance to nearest upland boundary (km)	0	4.665	0.380	0.727
LFD	Linear feature density (km/km ²)	0	26.826	2.148	2.796
Well	Proportion of oil and gas wells	0	0.250	0.015	0.026
Burn	Proportion of burns	0	0.785	0.019	0.086
Bog	Proportion of bog	0	0.848	0.164	0.146
Anthro	Proportion of anthropogenic	0	0.557	0.017	0.041
DecFor	Proportion of deciduous forest	0	0.959	0.096	0.157
Fen	Proportion of fen	0	0.971	0.110	0.125
MixFor	Proportion of mixed forest	0	0.379	0.049	0.053
UplCon	Proportion of upland conifer forest	0	0.991	0.522	0.228
Water	Proportion of water	0	1.000	0.023	0.091
OpenHab	Proportion of open habitat	0	0.081	0.001	0.002

Table 2. Mixed-effects logistic regression models, including measures of model support (Akaike's information criterion (AIC) and Δ AIC), describing habitat selection by black bears (*Ursus americanus*) during the calving season of woodland caribou (*Rangifer tarandus caribou*) in the Cold Lake Air Weapons Range, northeastern Alberta, Canada, 2001–2003.

Model	Variables ^a	<i>k</i>	AIC	Δ AIC
Global	DRivk + DPerlak + DSeisk + DRoadk + DPipek + LFD + LFD² + Well + DUplk + DecFor + DecFor² + Anthro + Bog + Fen + Burn + UplCon + MixFor + MixFor² + (1 Bear ID)	21	22 619	0
Czertwytynski ^b	UplCon + DecFor + DecFor ² + DRoadk + DRivk + DPerlak + DWellk + DLFk + (1 Bear ID)	11	23 117	498
Anthropogenic	DSeisk + DRoadk + DPipek + LFD + LFD ² + Well + Anthro + (1 Bear ID)	10	23 274	655
Natural	DRivk + DPerlak + DUplk + DecFor + DecFor ² + Bog + Fen + Burn + UplCon + MixFor + MixFor ² + (1 Bear ID)	14	25 563	2944
Caribou	Bog + Fen + DUplk + (1 Bear ID)	6	26 027	3408

Note: The best model is shown in boldface type. *k* is the number of parameters in the model.

^aBear ID refers to the identification code of the individual black bear. For other variable abbreviations see Table 1.

^bThe variables DWellk and DLFk were only included in the Czertwytynski model.

lection by black bears might only provide us with broad patterns of selection (Boyce et al. 2003), supporting the well-known generalist nature of these animals (Young and Ruff 1982; Czertwytynski 2007; Garshelis 2009), and potentially masking any impact that individual black bears might be having on caribou. Consequently, we assessed habitat selection for bears individually. We limited this analysis to testing the hypothesis that black bears select areas with a high proportion of bogs and (or) fens and areas farther from upland habitat edges, i.e., those habitat types that are known to be selected by caribou. We used the same eight locations per bear daily that were selected for the population-level analysis. GPS locations of black bears were then compared with random locations, generated using a 1:1 ratio, to estimate a used-available RSF (Johnson et al. 2006). Random locations for each individual bear were drawn from within the 100% MCP encompassing all of the calving-season locations collected for that

bear. The same model (Bog + Fen + DUplk) was tested 15 times, i.e., once for each individual black bear. The sign, magnitude, and significance (i.e., confidence intervals not spanning 0) of the coefficients for each of the variables within the model were assessed as evidence for or against the hypothesis that black bears were selecting habitats preferred by caribou.

Spatial overlap of black bears – caribou

For this analysis, we randomly selected 1 location per black bear daily during the calving seasons of 2001, 2002, and 2003, yielding 1275 bear locations. We chose to include a slightly larger sample interval for the caribou data (i.e., 2000–2004, as opposed to 2001–2003 for black bears) to increase the sample size to 262 caribou locations within the study area and sample interval.

We used logistic regression to estimate coefficients for latent selection difference (LSD) functions (Mueller et al.

2004; Fischer and Gates 2005; Czetwertynski 2007; S. Lele, personal communication) to contrast the differences in habitat selection between caribou and black bears during the calving season. This method allows for direct comparisons of habitat selection between two groups of interest and produces quantifiable measurements of strength of relationships (Czetwertynski 2007). A key assumption of this method is that all habitat types should be equally available to both species within the study area; locations of black bears and caribou in Fig. 1 show that this assumption was not violated in our study area. The model is assumed to conform to the following form:

$$[1] \quad w(\mathbf{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_i x_i)$$

where $w(\mathbf{x})$ represents the relative probability of black bears (coded as 1) occurring on the landscape compared with caribou (coded as 0) (Czetwertynski 2007). The β_i represents the selection coefficient for each predictor variable (x_i) from a vector of covariates (\mathbf{x}), and should be interpreted as the relative difference in selection between two species and not the selection or use of a given habitat type (Czetwertynski 2007). This model does not work with individuals as random factors and consequently does not correct for an unbalanced sampling design. We estimated standard errors (SE) using the Huber–White sandwich estimator (White 1980) grouping data by individual bear or caribou, i.e., we assumed that observations were independent across clusters (between bears or caribou) but not within clusters (data points associated with a given bear or caribou).

We used LSDs to assess spatial separation between caribou and black bears during the calving season by evaluating the relative difference in selection for bog, fen, and deciduous and conifer forests. We further assessed spatial separation by comparing the effect of distance to all-season road, rivers and streams, and upland habitat edge on the selection of black bears versus caribou. The exponentiated coefficients from this analysis indicate that with every unit increase in the proportion of a cover type or in the distance to a given feature, the relative selection of such a landscape feature by black bears compared with caribou is increased or reduced by $x\%$. For example, if $\beta = -2.4$ for covariate A, then the effect of the covariate was calculated as $[1 - \exp(-2.4)] \times 100 = 91$, and interpreted as with every unit increase in covariate A, relative risk of selection of such habitat by black bears compared with caribou decreased by 91%. The methods for interpreting the coefficients have been adapted from Czetwertynski (2007).

All statistical analyses were performed in R version 2.10.1 for Windows (R Development Core Team 2009).

Results

The 1 h GPS fix rate for 15 black bears captured and GPS radio-collared during the 2001–2003 caribou calving seasons provided 21 788 locations, ranging from 1 to 24 locations per day with a mean of 17 locations per day. After randomly selecting 8 locations per bear daily, the number of GPS locations was 9791, with a range of 392–1384 locations per bear. Of the radio-collared bears, 9 were females and 6 were males. The mean age of bears was 8.6 years (range = 4–21 years).

Table 3. Best mixed-effects logistic regression model describing resource selection by black bears (*Ursus americanus*) during the calving season of woodland caribou (*Rangifer tarandus caribou*) in the Cold Lake Air Weapons Range, northeastern Alberta, Canada, 2001–2003 (Table 2).

Variable	β	SE	P
DRivk	−0.247	0.028	<0.001*
DPerlak	0.098	0.016	<0.001*
DSeisk	−0.313	0.060	<0.001*
DRoadk	−0.230	0.007	<0.001*
DPipek	−0.129	0.025	<0.001*
LFD	0.110	0.021	<0.001*
LFD ²	−0.005	0.001	<0.001*
Well	2.429	0.957	0.011*
DUpk	−0.131	0.026	<0.001*
DecFor	0.511	0.468	0.275
DecFor ²	−2.248	0.604	<0.001*
Anthro	1.477	0.641	0.021*
Bog	−2.489	0.246	<0.001*
Fen	−1.197	0.253	<0.001*
Burn	1.910	0.312	<0.001*
UplCon	−0.372	0.212	0.079
MixFor	6.128	1.120	<0.001*
MixFor ²	−34.426	4.618	<0.001*

Note: For variable abbreviations see Table 1. *, $P \leq 0.05$.

Population-level habitat selection by black bears

Of the five models that we estimated, the global model had the lowest AIC value and thus the highest support from the tested set (Table 2). The global model included 16 covariates, including natural and anthropogenic cover types, distance to three types of anthropogenic linear features, distance to upland edges, distance to two natural hydrological features, and linear feature density. There was little to no support for any of the remaining models tested.

Habitat selection by black bears in the CLAWR during the caribou calving season was positively influenced by the proportion of anthropogenic habitat, oil and gas wells, and burnt forest (Table 3). Conversely, bears avoided areas with a high proportion of fen or bog habitat. Habitat selection by black bears was Gaussian relative to the proportion of deciduous and mixed-wood forests, indicating that bears preferred areas with intermediate levels of these types of vegetation. A similar type of relationship was found for the industrial linear feature density, suggesting that bears preferred areas with intermediate densities of these features. The relative probability of selection by black bears was highest near rivers and streams, upland boundaries, roads, pipelines, and seismic lines; conversely, black bears showed selection for areas farther from perennial lakes.

The k -fold cross-validation showed that the selected best RSF for black bears in the CLAWR during the caribou calving season performed well. The mean Spearman's rank correlation coefficient from 5-fold cross-validation was 0.9879 ($P < 0.05$), indicating that the model correctly predicted habitat use by bears.

Habitat selection by individual black bears

At the individual level, 13 bears showed avoidance of bogs

Table 4. Resource selection by individual black bears (*Ursus americanus*) ($n = 15$) during the calving season of woodland caribou (*Rangifer tarandus caribou*) in the Cold Lake Air Weapons Range, Alberta, Canada, 2001–2003.

Bear ID	Sex	Age (years) ^a	Bog		Fen		DUplk	
			β	P	β	P	β	P
7	Male	8	-1.734	<0.001*	0.494	0.356	-0.487	<0.001*
10	Male	5	-1.349	0.004*	4.504	<0.001*	-0.124	0.088
15	Female	10	-5.930	<0.001*	5.783	<0.001*	0.426	<0.001*
17	Male	7	-3.394	<0.001*	2.337	0.009*	-0.580	<0.001*
18	Female	6	1.289	0.065	-8.172	<0.001*	-2.044	<0.001*
21	Male	10	-4.528	<0.001*	-0.202	0.632	-0.080	0.095
117	Female	21	-11.676	<0.001*	-6.719	0.007*	-2.379	0.160
118	Female	5	-7.336	<0.001*	-5.507	<0.001*	-0.539	0.010*
119	Female	6	-7.680	<0.001*	0.819	0.161	-0.632	0.023*
121	Male	5	1.020	0.028*	0.825	0.044*	-0.727	<0.001*
123	Male	4	-0.782	0.001*	-5.150	<0.001*	-0.266	0.421
126	Female	6	-12.808	<0.001*	13.985	<0.001*	-1.601	0.363
129	Female	17	-3.161	<0.001*	2.023	0.010*	-0.967	0.003*
130	Female	9	-2.418	0.002*	0.668	0.322	-0.789	<0.001*
131	Female	10	-4.358	<0.001*	-0.501	0.283	-0.288	0.159

Note: The same model (Bog + Fen + DUplk) was fitted for each bear. Habitats preferred by caribou significantly selected for by black bears are shown in boldface type. *, $P \leq 0.05$.

^aAge was estimated and reported as of 2001.

of black spruce, 1 bear showed selection for this type of habitat, and 1 bear showed neither avoidance nor selection (Table 4). Alternatively, six bears showed selection for tamarack-dominated fens, while four bears avoided this type of habitat and five bears showed neither avoidance nor selection. The relative probability of use significantly decreased with increasing distances from an upland boundary for eight bears, as evidenced by the negative coefficient for this variable. In general, this indicates that although some bears showed selection for fens and to a lesser extent for bogs, this may have been confined to peripheral rather than core peatland (fen and bog) habitat. However, the opposite pattern was observed for bear 15, suggesting that some bears forage or roam farther from uplands and into core caribou habitat.

Of the six bears that selected caribou-preferred habitats (i.e., fen, bog, or away from an upland boundary), three were males and three were females, suggesting no sex-bias, albeit based on a small sample size. Bears that selected for caribou-preferred habitats ranged between 5 and 17 years, with four bears being between 5 and 7 years old and two older bears being at 10 and 17 years old.

Spatial overlap of black bears – caribou

We found that bear observations were most common in upland habitats (65% of locations) during the calving season, whereas caribou were most common in peatland habitats (66% of locations).

Our assessment of habitat selection by black bears relative to caribou showed that bears were less likely to use bogs, fens, and upland conifer stands compared with caribou (Table 5). With every unit increase in the proportion of these cover types, relative selection of such habitat by black bears compared with caribou was reduced by 98%, 99%, and 91%, respectively. Conversely, black bears were more likely to select deciduous forest stands than caribou. Finally, with an increase of 2.5 km in the distance to a river or stream, road, or upland boundary, relative risk of selection of such landscape

features by bears compared with caribou was reduced by 85%, 65%, and 78%, respectively.

Discussion

Studies that aim to assess ecological interactions between predators and woodland caribou are faced with the conundrum that caribou are usually an incidental prey species for predators, and thus are not important to predators at the population level. However, even limited incidental predation can have a significant impact on caribou populations (Wittmer et al. 2005; Latham et al. 2011). Because caribou usually spatially separate from alternative prey and predators (e.g., Bergerud et al. 1984; James et al. 2004), population-level analyses of habitat selection and spatial overlap often report that predators select different habitats than incidental prey such as caribou. Thus, although population-level habitat analyses can provide insights into what broad-scale factors predators select (i.e., they describe the mean pattern of habitat selection within the population), they might miss important interactions between individual animals and characteristics of their home range (Boyce et al. 2003; Forester et al. 2009), such as interactions with incidental prey.

The results from our population-level assessment of habitat selection by black bears during the caribou calving season similarly showed that black bears and caribou selected different habitats. We found that black bears selected rivers and streams, well-drained upland mixed woods, and various industrial features associated with this type of forest (also see Young and Ruff 1982; Czetwertynski 2007). Previous studies have reported the importance of rivers and streams for black bears in spring (e.g., Lyons et al. 2003), whereas Czetwertynski (2007) states that high use of industrial linear features in CLAWR was likely related to the high abundance of forage along these features and because hunting was prohibited in this area allowing bears to exploit this resource unmolested. In contrast, caribou showed strong selection for bogs and fens relative to black bears (also see Bradshaw et al. 1995;

Table 5. Latent selection difference (LSD) function model comparing the relative habitat selection by black bears (*Ursus americanus*) (coded as 1) and woodland caribou (*Rangifer tarandus caribou*) (coded as 0) during the caribou calving season in the Cold Lake Air Weapons Range, northeastern Alberta, Canada, 2000–2004.

Variable	β	SE	<i>P</i>	Relative selection (%) ^a
Bog	-4.086	1.396	0.003*	98
Fen	-5.191	1.157	<0.001*	99
DecFor	10.891	2.971	<0.001*	>100
UplCon	-2.423	1.005	0.016*	91
DRivk	-0.771	0.155	<0.001*	85
DRoadk	-0.417	0.032	<0.001*	65
DUplk	-0.614	0.093	<0.001*	78

Note: For variable abbreviations see Table 1. *, $P \leq 0.05$.

^aFor ease of interpretation, relative selection was calculated as $\exp(\beta)$ when $\beta > 0$ and as $[1 - \exp(\beta)] \times 100$ when $\beta < 0$. Relative selection for variables with $\beta < 0$ should be interpreted as follows: with every unit increase in the proportion of the cover type or for every 2.5 km increase in the distance to the landscape feature, the relative selection of such a landscape feature by black bears compared with caribou is reduced by $x\%$.

Stuart-Smith et al. 1997) and have previously been reported to avoid industrial linear features (Dyer et al. 2001). These results are consistent with the hypothesis that caribou in the boreal forest attempt to minimize predation risk by spatially separating themselves from predators by selecting peatlands (Cumming et al. 1996; James et al. 2004). However, despite evidence confirming the importance of black bears as predators of caribou, particularly calves (Mahoney et al. 1990; Ballard 1994), this analysis provides little insight into the interactions that create the potential for caribou–bear encounters and predation events.

A number of recent studies have demonstrated the occurrence of individual specialization within animal populations (e.g., Bolnick et al. 2003; Urton and Hobson 2005; Robichaud 2009), with important ecological, evolutionary, and conservation implications. Our assessment of habitat selection by individual black bears showed that although most bears showed selection for upland mixed woods and industrial features such as pipelines, roads, and well-pads, some individuals showed selection for habitats similar to those used by caribou. Most notably, six of the bears showed selection for tamarack-dominated fens and one bear selected bogs of black spruce (although arguably selection was mostly confined to the periphery rather than the core of these habitats). The habitat preferences of two of the six bears changed in the summer (15 July to 14 August); one bear avoided caribou-preferred habitats, whereas one bear showed neither selection nor avoidance of these habitats. In the autumn (15 August until denning), two of the six bears avoided caribou-preferred habitats, whereas one bear showed neither selection nor avoidance of these habitats. These results indicate that some individual bears might focus their foraging efforts in peatlands (at least seasonally), rather than the upland forest preferred by most individuals. Although we did not assess food habits of black bears in CLAWR, and consequently do not know the main food resources for bears, it is probable that bears that specialize on foraging in peatlands are responsible for at least some of the predation on caribou calves (as has been shown elsewhere in North America; e.g., Mahoney et al. 1990; Ballard 1994). Horsetails (genus *Equisetum* L.)

also may be an important food for bears in peatlands in spring (Czetwertynski 2007); however, most bear-preferred vegetation is associated with uplands (Garshelis 2009).

The observed variation in habitat selection by individual black bears could be the result of a number of factors including spatial variation in food supply within home ranges, phenotypic or behavioural differences that affect foraging success, or social learning (Estes et al. 2003). Because previous studies have reported that caribou calves are most vulnerable to predation by bears during their first month of life (Bergerud 1971; Mahoney et al. 1990), we confined our assessment of habitat selection by black bears to the caribou calving season. Adult bears that specialize on foraging in peatlands during this period might develop a search image for calves when they are most vulnerable to predation. If an adult bear is successful at killing calves in peatlands during the calving season, then that individual might continue to forage in peatlands in subsequent years. Similarly, it is possible that cubs of mothers that have learned to hunt successfully in peatlands might develop a search image for caribou calves (Nielsen 2005). Alternatively, Czetwertynski (2007) found that female black bears in CLAWR were territorial with other females, especially when they had cubs. Accordingly, as the density of bears increases, the amount of unoccupied food-rich habitat (i.e., upland mixed woods) will decrease until all that is left is food-poor habitats, such as bogs and fens. To avoid the risks associated with foraging in food-rich occupied territories, less dominant individuals may be forced to live and forage in peatlands. Regardless of the specific mechanism, our results suggest that approximately one-third of the black bears in CLAWR forage in habitats used by caribou during the calving season.

Although our assessment of individual bears showed high use of peatlands by some bears, our assessment of spatial overlap showed substantive differences in selection by bears for peatland habitats relative to caribou, i.e., bears were significantly less likely to be found in peatlands than caribou. This pattern also was apparent for upland conifer stands, likely because the AGCC classification system included stands of jack pine and mature black spruce that have

previously been shown to be selected by caribou (Bradshaw et al. 1995; Dzus 2001). These results, together with the population-level analysis of habitat selection by black bears, imply that woodland caribou in northeastern Alberta maintain spatial separation from not only wolves and alternative prey (James et al. 2004), but also from black bears. However, those individual bears that deviate from the population-level pattern and select peatlands might be contributing to the high mortality of caribou calves in Alberta.

Black bears have been shown to be significant predators of ungulate neonates across much of North America. In Alberta, it has been suggested that bears might be an important mortality factor for calves of woodland caribou, and thus contributing to population declines for some herds. Our results suggest that black bears spend the majority of their time foraging in upland mixed woods and only a few of the bears forage in peatlands. However, it is important to note that this pattern holds for other significant predators of caribou (adults and calves), such as wolves. Despite this pattern, management actions to conserve caribou often include direct removal of wolves or reductions in densities of moose, elk, and deer to indirectly reduce wolf numbers. Declines in caribou populations in Alberta have resulted from a combination of high adult female and calf mortalities, and subsequent low recruitment. Based on our results, we speculate that approximately one-third of black bears in northeastern Alberta may be contributing to high mortality of caribou calves. Consequently, management actions to conserve woodland caribou must consider the entire suite of potential predators rather than focusing solely on wolf control.

Acknowledgements

Funding and support for this project was provided by the Alberta Caribou Committee (ACC), Alberta Sustainable Resource Development (ASRD), and Canadian Association of Petroleum Producers (CAPP). We thank the Alberta Conservation Association, Natural Sciences and Engineering Research Council of Canada, Sustainable Forest Management Network, Alberta-Pacific Forest Industries, Pope and Young Club, Alberta Bowhunters Association, Canadian Wildlife Federation, Alberta Professional Outfitters Society, Alberta Fish and Game Association, and Safari Club International for support of the black bear project. We thank S. Czetwertynski, R. Lemieux, and F. Schmiegelow for assistance with black bear data. We also thank personnel at the Department of National Defence (4-Wing, Cold Lake, Alberta) for access to the Cold Lake Air Weapons Range during the field component of this study. We thank E. Dzus, D. Hervieux, and M. Russell for assistance with caribou data, and S. Lele for his ideas on the latent selection difference functions. Finally, we thank S. Boutin and two anonymous reviewers for providing comments on an earlier draft of the manuscript.

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