Biological Conservation 144 (2011) 2637–2646

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou

J.L. Polfus [a,*], M. Hebblewhite [a], K. Heinemeyer [b]

[a] Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA
[b] Round River Conservation Studies, 284 West 400 North, Suite 105, Salt Lake City, UT 84103, USA

ARTICLE INFO

Article history:
Received 23 December 2010
Received in revised form 11 July 2011
Accepted 17 July 2011
Available online 10 August 2011

Keywords:
Cumulative effect
Habitat selection
Potential habitat
Rangifer tarandus caribou
Resource selection functions (RSF)
Zone of influence (ZOI)

ABSTRACT

Understanding the impact of indirect habitat loss resulting from avoidance of human infrastructure is an important conservation priority. We evaluated resource selection for 10 global positioning system collared northern mountain woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada, with seasonal resource selection functions (RSF) developed at the second-order (landscape) and third-order (within home range) scales. To estimate how much habitat was lost due to avoidance, we estimated the zone of influence (ZOI) around multiple developments and modeled realized and potential habitat. Potential habitat was approximated by removing the ZOI from RSF models. By calculating the spatial difference between potential and realized habitat we estimated the amount of indirect habitat loss. Caribou displayed hierarchical avoidance of development, with the greatest avoidance occurring at the second-order. During both seasons caribou avoided high-use roads by 2 km and low-use roads by 1 km. In winter, caribou avoided town by 9 km compared to 3 km in summer. However, in summer caribou avoided mines by 2 km and cabins and camps by 1.5 km, while in winter when human activity was low, avoidance of these features was minor. As a result of avoidance of the cumulative ZOI, approximately 8% and 2% of high quality habitat was lost in the study area in winter and summer, respectively. Our study provides an approach to identify the extent and quality of habitat influenced by indirect avoidance. Conservation efforts should prioritize protecting areas of high quality habitat degraded by avoidance in the vicinity of human development.

1. Introduction

Expanding human development is a global conservation concern and a mounting problem in resource-rich northern ecosystems. The total land area impacted by human activities is projected to increase dramatically by 2050 (UNEP, 2001). While direct habitat loss is the primary cause of wildlife population decline and extinction (Brooks et al., 2002), indirect habitat loss due to displacement from preferred habitats near human activity or infrastructure also has potential to negatively influence population abundance (Patthey et al., 2008). Patterns of avoidance can vary with respect to species, season, habitat quality and the intensity of human disturbance. Further, different types of human disturbance, such as roads and settlements, are likely to have varying degrees of influence on the strength of avoidance and have the potential to interact in a cumulative manner with habitat quality and local population dynamics to influence patterns of habitat selection. Habitat selection forms the basis for understanding how multiple development types affect populations over time and space (Aarts et al., 2008), yet there have been few quantitative assessments of the extent and quality of indirect habitat loss that occurs due to avoidance.

Caribou and reindeer (*Rangifer tarandus*) are habitat specialists and are sensitive to anthropogenic activities across their circumpolar range (Vors and Boyce, 2009). Humans directly affect *Rangifer* through hunting mortality, habitat alteration and barriers to movement (Dyer et al., 2002; Weir et al., 2007). In addition, caribou and reindeer avoid areas close to roads, resource development, infrastructure and human settlements (Dyer et al., 2001; Vistnes and Nellemann, 2008). The northern mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) occurs throughout the Yukon Territory, Northwest Territories and northwestern British Columbia (BC). In winter, northern mountain woodland caribou forage on terrestrial lichen in forests and alpine windswept areas (Gustine and Parker, 2008; Johnson et al., 2000) and primarily forage on herbaceous vegetation and lichen in alpine environments in summer (Ion and Kershaw, 1989; Oosenbrug and Theberge, 1980), yet forage is not commonly considered a limiting factor

* Corresponding author. Tel.: +1 970 309 5698; fax: +1 406 243 4557.
E-mail addresses: jeanpolfus@gmail.com (J.L. Polfus), mark.hebblewhite@cfc.umt.edu (M. Hebblewhite), kim@roundriver.org (K. Heinemeyer).

0006-3207/$ - see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2011.07.023

for northern mountain woodland caribou (Hegel et al., 2010). Recent population declines and varying degrees of direct and indirect habitat loss, fragmentation and human-induced changes to predator–prey communities prompted federal managers to list northern mountain woodland caribou as a species of special concern in 2004 under the Species at Risk Act (COSEWIC, 2002).

Studies that examine avoidance of human development by caribou or reindeer vary greatly in methodology, with techniques ranging from aerial and ground surveys, pellet counts, measurements of lichen biomass and height, movement rates and analyses of telemetry data (Dyer et al., 2001; Vistnes and Nellemann, 2001; Vistnes et al., 2008; Weir et al., 2007). These disparate techniques have lead to political and scientific controversy regarding the effect of human activity on caribou habitat use, especially when stakeholders have vested interest in the interpretation of avoidance distances (Wolfe et al., 2000). Importantly, recent research suggests that the scale of assessment has a strong influence on the probability of detecting impacts (Vistnes and Nellemann, 2008). For example, while many small-scale behavioral disturbance studies indicate minimal effects from human development, large-scale studies in the same areas often show significant changes in habitat use patterns (Joly et al., 2006; Vistnes and Nellemann, 2008). Habitat selection studies often identify zones of influence (ZOI) that represent the area affected by human disturbance. These ZOI buffers are especially important when used to measure cumulative effects, mitigate impacts or inform population models (Sorensen et al., 2008), but differences in methods can lead to controversies about buffer widths, significance and the type of response measured (Gunn et al., 2011). There is a growing need for a consistent approach to monitor avoidance that can be applied across scales for species that are affected by human development. Our objectives were to estimate a biologically relevant ZOI around human developments and determine the cumulative indirect impacts of development on habitat selection of the Atlin herd of northern mountain caribou.

We used resource selection function (RSF) models to estimate caribou habitat selection by statistically comparing use of resources and conditions relative to availability (Manly et al., 2002). To examine if the cumulative effects of human developments have different consequences at multiple scales and seasons (Houle et al., 2010) we developed seasonal RSF models at Johnson's (1980) second-order (landscape) and third-order (within home range) scales. Since human developments are often correlated in space, they can have confounding effects when modeled together. Therefore, to incorporate the cumulative impact of different types of development into our RSF models we used empirical data to estimate the biologically relevant ZOI around roads, mines, cabins, camps and towns. This approach builds on previous techniques that based the width of a ZOI buffer on expert opinion or published literature (Florkiewicz et al., 2007; Johnson et al., 2005). We hypothesized that the ZOI would vary between season and development type and that caribou would exhibit the strongest avoidance of the ZOI at the second-order scale because caribou are known to respond to risk in a hierarchical fashion (Rettie and Messier, 2000). Thus, at the third-order scale we predicted that human developments would have less of an effect on selection because of predominant avoidance at the larger scale (Johnson et al., 2001).

To quantify the amount of habitat affected by avoidance of the ZOI we spatially analyzed predictions of realized and potential habitat (Hirzel and Le Ley, 2008; Nielsen et al., 2010). We considered realized habitat to be the current habitat selected by caribou when avoidance of the cumulative ZOI was included in the RSF models (Hirzel and Le Ley, 2008). We estimated potential habitat by removing the ZOI from the RSF models (Johnson et al., 2005). Thus, potential habitat can be considered the habitat caribou would select if they did not avoid the cumulative ZOI (Hirzel and Le Ley, 2008; Soberón, 2007). We assumed that areas of high probability of use were biologically important and thus represented high quality habitat (Railsback et al., 2003). Finally, we calculated the spatial differences between potential and realized habitat to estimate the amount and quality of habitat lost due to avoidance of the cumulative effects of multiple human developments (Johnson et al., 2005; Nielsen et al., 2010).

2. Materials and methods

2.1. Study area

The study area encompassed 11,594 km^2 within the Atlin northern mountain woodland caribou herd's home range located between Atlin Lake and Teslin Lake along the Yukon-BC border (Fig. 1). Elevations ranged from 660 to 2000 m. The climate is typified by long, cold winters and short, warm summers. Annual precipitation in Atlin is approximately 33 cm (MacKinnnon et al., 1999). Low to mid-elevation boreal forests include open coniferous stands dominated by lodgepole pine (*Pinus contorta latifolia*), subalpine fir (*Abies lasiocarpa*) and white spruce (*Picea glauca*). Deciduous stands of trembling aspen (*Populus tremuloides*), black cottonwood (*Populus balsamifera trichocarpa*), alder (*Alnus tenuifolia*) and willow (*Salix* spp.) occupy valley bottoms. Alpine habitats (above 1500 m) consist of extensive areas of rolling alpine tundra characterized by sedge, Altai fescue (*Festuca altaica*) and lichens. Other ungulates include moose (*Alces alces*), mountain goats

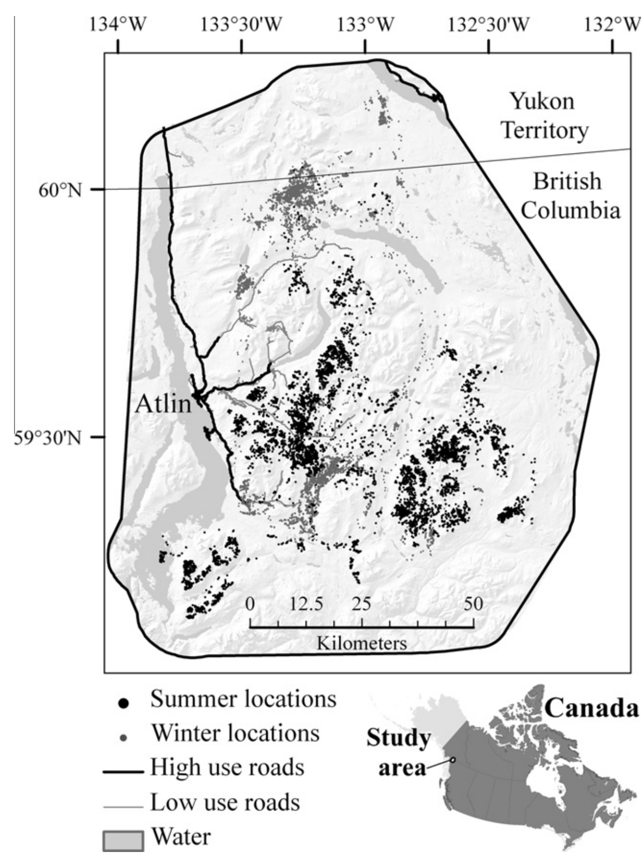

Fig. 1. Locations of 10 global positioning system (GPS) collared northern mountain woodland caribou in North America on the border of the Yukon Territory and British Columbia, Canada. Locations are shown for summer (May 16–November 14) and winter (November 15–May 15) between 2000 and 2002. The study area represents the 11,594 km^2 buffered minimum convex polygon of all known caribou locations.

(*Oreamnos americanus*) and Stone's sheep (*Ovis dalli stonei)*. The large mammal predator community consists of grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), wolverines (*Gulo gulo*), wolves (*Canis lupus*), coyotes (*Canis latrans*) and lynx (*Lynx canadensis*).

The study area composes approximately a quarter of the traditional territory of the Taku River Tlingit First Nation (TRTFN). The town of Atlin (59°35′N, 133°40′W) is the largest settlement in the study area with approximately 350 residents. Paved roads extend out from the town (98.1 km) and unimproved gravel and dirt roads (398.4 km) and ATV trail systems (739.3 km) connect placer and hardrock mines ($n \sim 94$). Timber harvest is limited to a small-scale operation near the town of Atlin. The total road density within 10 km of Atlin is 0.53 km km^{-2} while the overall road density across the study area is 0.11 km km^{-2}. Caribou hunting includes First Nation harvest and a combined limited entry hunt and guide-outfitter quota of 10 males/year. First Nation harvest is assumed to be small, due to a voluntary hunting ban in place since 1993.

2.2. Animal capture

Eight adult female and two adult male caribou from the Atlin herd were monitored with global positioning system (GPS) telemetry collars (GPS 2000, LOTEK, Aurora, ON) between January 2000 and January 2002 by the Ministry of Water, Land, and Air Protection of British Columbia. Caribou were captured by helicopter net-gunning according to Wildlife Radio-Telemetry, Standards for Components of BC's Biodiversity No. 5, RIC 1998. Five GPS collars were deployed 10 January 2000 and scheduled to self-release in November 2000. The five GPS collars were retrieved, refurbished and re-deployed on new individuals on 13 February 2001 and self-released between 29 November 2001 and 27 January 2002. Collars were scheduled to attempt a location every 4 h. Because GPS fix success was >90%, we did not need to correct for habitat-induced bias in the RSF models (Frair et al., 2004).

2.3. Cumulative zone of influence

To assess the cumulate effects of multiple development types on caribou habitat selection, we estimated the ZOI around developments that caribou avoided (Johnson et al., 2005). This was necessary because of high collinearity between development types (roads, mines, cabins and hunting camps and the town of Atlin, Table 1). We estimated buffer width by breaking distance to each development type into distance categories (i.e., 0.5, 1, 1.5 km, etc.). For each season and development type we chose the smallest distance category possible that retained at least one caribou location within each division. This made comparisons between used and available points possible within each distance category (Manly et al., 2002). Thus, distance category divisions ranged from 0.25 km to 3 km depending on the development type and season (Fig. 2). Each distance category was evaluated for each development type, one by one, as a categorical variable in the top seasonal RSF model. Selectivity coefficient estimates for each distance category and for each development type were recorded. Negative coefficients indicated avoidance of the distance category and neutral or positive coefficients indicated caribou use of the distance category was proportional or greater than expected based on availability. We considered the biologically relevant ZOI buffer around each development type to be the distance category prior to where the standard errors of the selectivity coefficient first crossed zero (i.e., Frair et al., 2008). We then merged the ZOI buffer for each development type to create a cumulative ZOI that was incorporated into the seasonal RSF models as a binary variable and indicated when a used or available location fell within or outside of the ZOI (Florkiewicz et al., 2007). This covariate represented the cumulative effect of human development and accounts for the high correlation between the 'distance to' development variables.

Table 1
Pearson's correlation *r* between distance to low and high use roads, the town of Atlin, cabins and hunting camps and placer and hardrock mines in the home range of the Atlin herd of northern mountain woodland caribou in northern British Columbia. Summer (May 16–November 14) variables shown in italics in the bottom left and winter (November 15–May15) variables shown in top right.

Distance to (km)	Low use roads	High use roads	Town (Atlin)	Cabins and camps	Mines
Low use roads	1	0.811	0.656	0.320	0.484
High use roads	*0.872*	1	0.527	−0.009	0.138
Town (Atlin)	*0.865*	*0.937*	1	0.750	0.794
Cabins and camps	*0.714*	*0.419*	*0.459*	1	0.870
Mines	*0.728*	*0.435*	*0.494*	*0.861*	1

2.4. Second-order resource selection function models

We developed RSFs at the second- and third-order scales during winter (15 November–15 May) and summer (16 May–14 November). Seasons were defined based on caribou use of elevation. The use-availability design is an approximation of a true probability function because use is compared to available locations, not true absences (Keating and Cherry, 2004). However, the relative probabilities are still useful for ranking habitat quality because the design approximates the logistic discriminant function (Johnson et al., 2006). We estimated RSFs at the second-order scale with a use-availability design described in Manly et al. (2002) by comparing resource covariates at used GPS locations to random available locations. We sampled availability using a 1:1 ratio of used to available locations within the pooled 99% fixed kernel seasonal home ranges for all collared caribou. Home ranges were estimated using Home Range Extension (Rodgers and Carr, 2002) with a smoothing factor of 0.7 × the reference smoothing factor (h_{ref}; winter = 0.229, summer = 0.218) which is appropriate for large sample sizes and short-interval GPS data (Hemson et al., 2005). To account for unbalanced sample sizes between individual caribou and for temporal and spatial autocorrelation, we evaluated selection at the second-order using generalized linear mixed models (GLMM) with a random intercept for each animal (Bolker et al., 2009; Gillies et al., 2006). The form of the mixed-effects model for location (i) and individual caribou (j) with a random intercept is given as:

$$w^{*}(x)_{ij} = \beta_0 + \gamma_{0j} + \beta_1 x_{1ij} + \cdots + \beta_n x_{nij} + \epsilon_{ij}$$

where $w^{*}(x)$ is proportional to the predicted relative probability of use as a function of covariates $x_1 \ldots n$, and $\beta_1 \ldots n$ are the selection coefficients estimated from mixed-effects logistic regression (Manly et al., 2002). Note that because of the use-available design, the fixed and random intercepts, $\beta_0 + \gamma_{0j}$, are meaningless and are often dropped by convention resulting in a relative probability, although they still affect the fixed-effect coefficients (Gillies et al., 2006). Mixed-effects models were estimated with STATA 11.0 (StataCorp, 2007) using xtlogit and GLLAMM (www.gllamm.org) depending on the ability of the model to converge.

2.5. Third-order resource selection function models

At the third-order scale, we used a matched-case control (also known as conditional) logistic regression to estimate the relative probability of caribou selection from one location to the next.

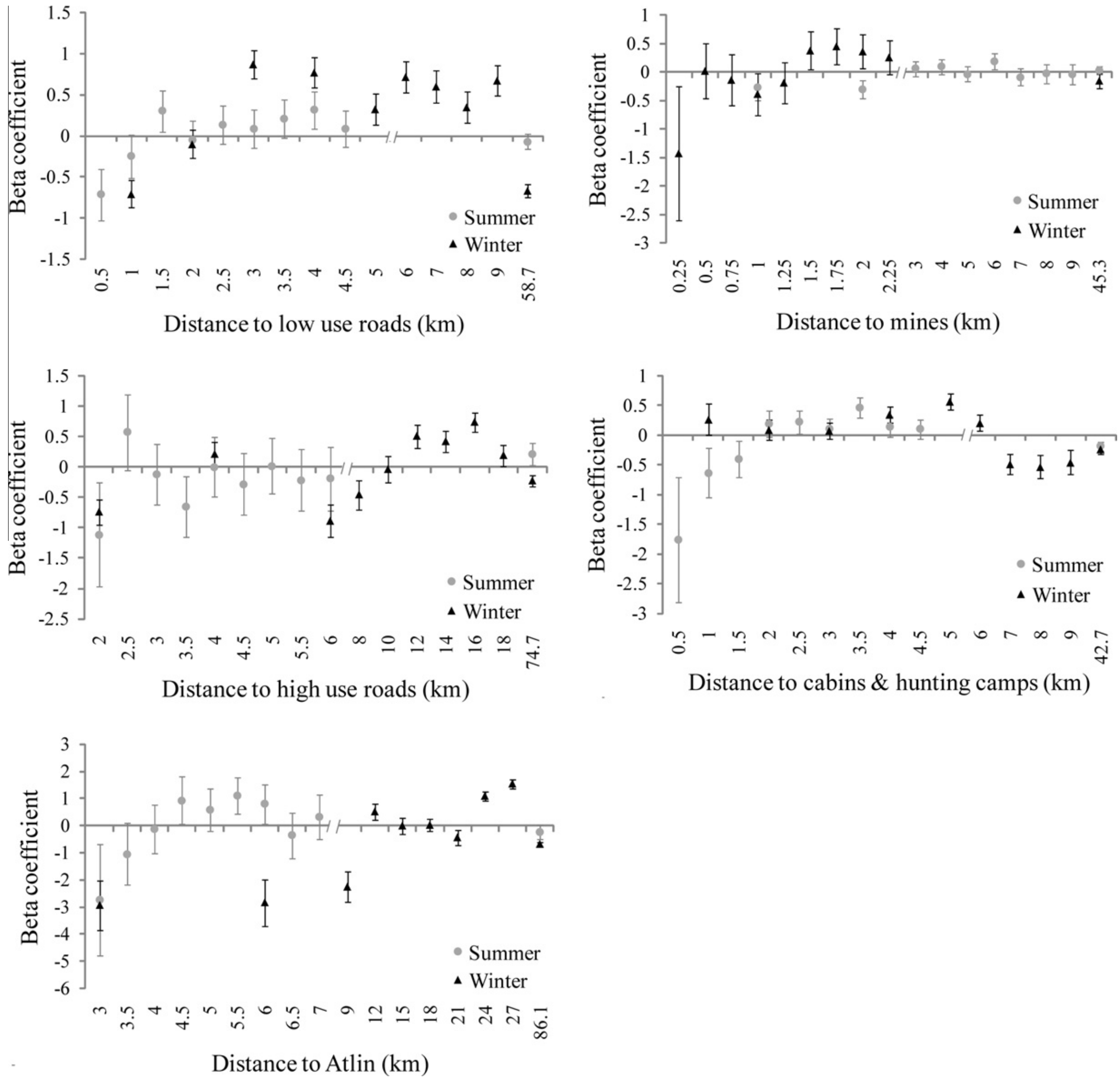

Fig. 2. Selectivity (beta) coefficients for distance (km) to high and low use roads, cabins and hunting camps, Atlin and mines divided into distance categories for the Atlin herd of northern mountain woodland mountain caribou in northern British Columbia from 2000 to 2002. Negative coefficients indicate avoidance, positive coefficients indicate selection. Distance category divisions were chosen to maintain at least one caribou location within each division. Thus, divisions differ between development types and seasons. The distance category prior to where the coefficient and associated confidence intervals changed signs was the distance that was used to generate the binary variable of the cumulative zone of influence (ZOI). Refer to Table 1 for specific ZOI buffer values.

Matched-case control designs allow selection to be measured along movement paths rather than across the entire landscape (Compton et al., 2002). The limited spatial domain allows true absences to be compared to use (Duchesne et al., 2010). The unused locations were generated based on the bearing and empirical step-length and turning angle distributions of caribou movements and each unused location was matched to one used location (Compton et al., 2002). Thus, the unused location represented where a caribou could potentially have moved during the next time-step. The intercept is not estimated in the conditional likelihood because inferences about β_0 are not possible without knowledge of the sampling fractions (Hosmer and Lemeshow, 2000). Thus, implementation of mixed-effects conditional logistic regression is challenging (Duchesne et al., 2010). Instead of using mixed-effect models, we accounted for unbalanced sample sizes between animals using sample weighting to give equal weight to each animal. We weighted animals using the inverse of the probability that an individual caribou was included in the sample (Alldredge et al., 1998).

2.6. Potential habitat

To model potential habitat, which we defined as the habitat available to caribou when not constrained by avoidance of human developments, we generated RSFs without the ZOI and spatially mapped the predicted relative probability of use (standardized by dividing by the maximum) in ArcGIS 9.3.1 (ESRI, Redlands, CA). Because caribou use was observed within a landscape that already included human developments, it is difficult to remove the effects of humans by simply modeling caribou habitat without human developments. Thus, we assumed the effects of human developments were independent of other variables (i.e., were not confounding and had low correlation) and tested this assumption by comparing the model selectivity coefficients with and without the human ZOI covariate. We classified the realized and potential habitat maps into 10 quantiles from low to high quality. To quantify the change in habitat quality we subtracted the realized habitat rank from the potential habitat rank to measure how many ranks were lost in each cell when human developments were included in the model. The difference between the habitat ranks in the potential model and the realized model was used to determine the area (km^2) in each habitat rank category (1–10) that was lost due to the cumulative effect of existing human developments.

2.7. Resource covariates

We included resource covariates known or suspected to be important predictors of northern woodland caribou habitat selection in our analysis. All variables were screened for collinearity by calculating the Pearson's correlation between variables and using $|r| > 0.6$ as the threshold for removing a covariate (Hosmer and Lemeshow, 2000). Covariates of elevation (m), slope and hillshade were extracted from the TRIM digital elevation model (30 m^2 resolution). Vegetation community data were classified with Landsat TM satellite imagery into 13 landcover types at a 30 m^2 resolution (see Supporting data Table S1). Fires are relatively rare and small in the study area. However, to model mature stands of lodgepole pine with lichen groundcover known to be selected by northern mountain woodland caribou in winter (Florkiewicz et al., 2007; Gustine and Parker, 2008), we divided the lodgepole pine landcover class into a lodgepole/lichen category and burned lodgepole (stands that had burned since 1950) with data from provincial fire history. An average index of primary productivity (greenness) was spatially modeled by averaging 16-day composites of the Normalized Difference Vegetation Index (NDVI) at a 250 m^2 resolution from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) satellites across seasons (Pettorelli et al., 2005). Because snow is known to influence woodland caribou resource selection (Johnson et al., 2000), we generated percent snow cover from 8-day composites of maximum snow extent maps at 500 m^2 resolution produced by MODIS satellites (Hall et al., 2000). We divided the number of days snow occupied a cell by the number of days in the seasonal period to generate spatial models of percent snow cover. Winter snow cover was included in summer models to represent potential areas of residual summer snow patches (Ion and Kershaw, 1989).

Human development covariates included distance to roads, mines, cabins and hunting camps and the town of Atlin (km; BC geodatabase, www.geogratis.ca). Roads were categorized as high use (paved or plowed during winter) and low use (gravel/dirt roads excluding ATV trails). We updated the best available provincial road network data with GPS Routes from Garmin GPS Map60 handheld units. Mines were selected that reported work costs of >$50,000 to the Assessment Reporting Index System (www.empr.gov.bc.ca/mining/geoscience/aris) or were known to be active during the summer in the study area. Very few mines in the area were active in the winter.

2.8. Model evaluation

We used generalized additive models (GAM) to test whether coefficients were non-linear (Hastie and Tibshirani, 1990), and either transformed (e.g., square transformation) or used quadratic functions ($X + X^2$) to capture non-linearity in GLMMs (Hosmer and Lemeshow, 2000). The maximum of a quadratic relationship was used to estimate the intermediate value selected by caribou in the case of non-linear selection responses. To determine the importance of each variable, we used manual stepwise entry to select models and then compared a small subset of models using Akaike's information criterion (ΔAIC) to select a top model (Manly et al., 2002). Models were mapped in ArcGIS 9.3.1 at a 30 m^2 resolution. Model fit was evaluated using k-fold cross-validation (Boyce et al., 2002). Because RSFs describe the habitat selection of specific animals, we withheld 20% of data (i.e., $k = 5$) from each animal at random (Koper and Manseau, 2009). Predicted values were generated for the withheld caribou observations and assigned to 10 equal habitat rank bins of available relative probabilities calculated for each cross-validated model (Boyce et al., 2002). Spearman's rank (r_s) correlation was used to compare the RSF bins to the area-adjusted frequencies of predicted values in each bin; if an RSF model had high predictive power, then the frequency of caribou locations should have increased in higher habitat ranks.

3. Results

In total, 16,270 GPS locations were collected. Resource selection of males did not vary more or less than females (Chi-square test winter p-value = 0.455, summer p-value = 0.816), especially for the human ZOI buffer covariate (J. Polfus, *unpublished data*), thus all 10 GPS collared caribou (male and female) were pooled in models.

3.1. Zone of influence

At the second-order, the ZOI buffer, or the distance category where the human development coefficient changed signs, was similar between seasons for high and low use roads (2 km and 1 km, respectively; Table 2). In winter, the ZOI around Atlin was 9 km compared to 3 km in summer. There was low avoidance of mines and no avoidance of cabins and hunting camps in winter when human activity is generally limited. Alternately, in summer the ZOI was 2 km around mines and 1.5 km around cabins and hunting camps (Fig. 2). At the third-order, there was no significant avoidance of human developments during winter and only limited avoidance during summer (Table 2).

3.2. Second-order resource selection

At the second-order scale, inclusion of a random intercept for individual caribou marginally improved model fit over the fixed-effect RSF for both seasons (winter ΔAIC = 14.4, summer ΔAIC = 20.4; see Supporting data Table S2). Variation between individuals (winter 0.129, summer 0.115) was relatively high, but of a similar magnitude between seasons. Caribou showed significant avoidance of both the summer and winter cumulative ZOI buffer (Table 3). The summer and winter models had high predictive capacity with an average r_s of 0.997 (SD = 0.0054) and 0.993 (SD = 0.0108) respectively in 5-fold cross-validation.

Caribou showed strong seasonal differences in selection for resource and landcover covariates. In winter, caribou selected predominately mid-elevations of 1179 m and selected for lodgepole pine/lichen complexes, spruce/fir forests, and low elevation river valleys comprised of *Salix* spp. Caribou avoided krummholz, rock, burned lodgepole pine, alpine tundra, water and steep slopes. Caribou selected intermediate percent snow cover (60%) and high

Table 2
The biologically relevant zone of influence (ZOI) around multiple development types predicted with seasonal second-order and third-order resource selection function models for the Atlin herd of northern mountain woodland caribou in northern British Columbia. The ZOI is the distance category prior to where the selectivity coefficient and associated confidence intervals changed signs. Refer to Fig. 2 for details.

Development type	Second-order		Third-order	
	Winter	Summer	Winter	Summer
High use road	2.0 km	2.0 km	–	0.25 km
Low use road	1.0 km	1.0 km	–	0.25 km
Town (Atlin)	9.0 km	3.0 km	–	4.0 km
Mine	0.25 km	2.0 km	–	–
Cabins or camps	–	1.5 km	–	–

Table 3
Estimates of caribou selectivity (β) coefficients of the cumulative zone of influence (ZOI) and standard errors (SE) from second-order and third-order resource selection function models for the Atlin herd of northern mountain woodland caribou in northern British Columbia. Selection was measured in winter (November 15–May 15) and summer (May 16–November 14) from 2000 to 2002. Positive selectivity coefficients indicate selection and negative selectivity coefficients indicate avoidance. The most parsimonious winter third-order model did not include a cumulative ZOI buffer.

Covariate	Summer		Winter	
	Selectivity β	SE	Selectivity β	SE
Second-order ZOI	−0.478	0.0608	−0.954	0.0739
Third-order ZOI	−1.182	0.3375	–	–

values of hillshade, which represented selection for western slopes with high sun exposure. Conversely, in the summer, caribou resource selection shifted to higher elevations (1363 m) and caribou displayed strong selection for krummholz, alpine shrubland, alpine tundra, rock, slopes with high sun exposure and areas that had high percent snow cover in winter. Finally, caribou were negatively associated with water and steep slopes (see Supporting data Table S3).

3.3. Third-order resource selection

At the third-order scale, the summer model had high predictive capacity with an average r_s of 0.920 (SD = 0.0279) while the winter model had relatively low predictive performance with an average r_s of 0.704 (SD = 0.1295). In summer caribou avoided the cumulative ZOI buffer (Table 3), but the most parsimonious winter model did not include a cumulative ZOI buffer. Since inferences of resource selection at the third-order represented where caribou chose to move at the next location, we mapped selection within the 95th percentile of movement distance around used locations (2 km in winter, 2.7 km in summer). Within this extent in winter, caribou occurrence was positively related to lodgepole pine/lichen forests, spruce/fir forests, mixedwood stands and low slopes. In summer caribou selected alpine tundra, areas of high percent snow cover during the previous winter and high elevations (see Supporting data Table S4).

3.4. Potential habitat

At the second-order, seasonal RSF models were used to map habitat selection in the study area. Coefficients between the realized and potential GLMMs were very similar (see Supporting data Tables S5 and S6), confirming the validity of our assumption that removing human activity would approximate potential habitat. High quality habitat was defined as the top 30% of the probability of use predictions (RSF ranks 8–10) which included 68% of winter caribou locations and 80% of summer caribou locations. Roughly 30% of the study area was considered medium (RSF ranks 5–7) and 40% low (RSF ranks 1–4). In winter, the potential habitat map (modeled without the ZOI coefficient) had 276.2 km^2 more predicted high quality habitat, and 50 km^2 more medium quality habitat than the realized habitat map (Fig. 3). Thus, existing human developments were responsible for a 7.95% decrease in high quality habitat and 1.44% decrease in medium quality winter habitat available within the study area, mostly in the vicinity of the town of Atlin (Fig. 4). During winter at the third-order, there was no significant avoidance of human developments, thus the realized and potential maps were equivalent.

The overall effect of human development was weaker in summer. At the second-order, 60.8 km^2 of high quality habitat and 58 km^2 of medium quality summer habitat was avoided due to existing human development, which totaled 1.76% of the high quality habitat and 1.66% of medium quality habitat available (Fig. 3). At the third-order, caribou avoidance of the ZOI buffer resulted in the loss of 6.4 km^2 of high quality and 21.9 km^2 of medium quality summer habitat within the 3828 km^2 that was mapped along the movement paths of caribou. This resulted in the loss of 0.55% of high and 1.9% of medium quality summer habitat.

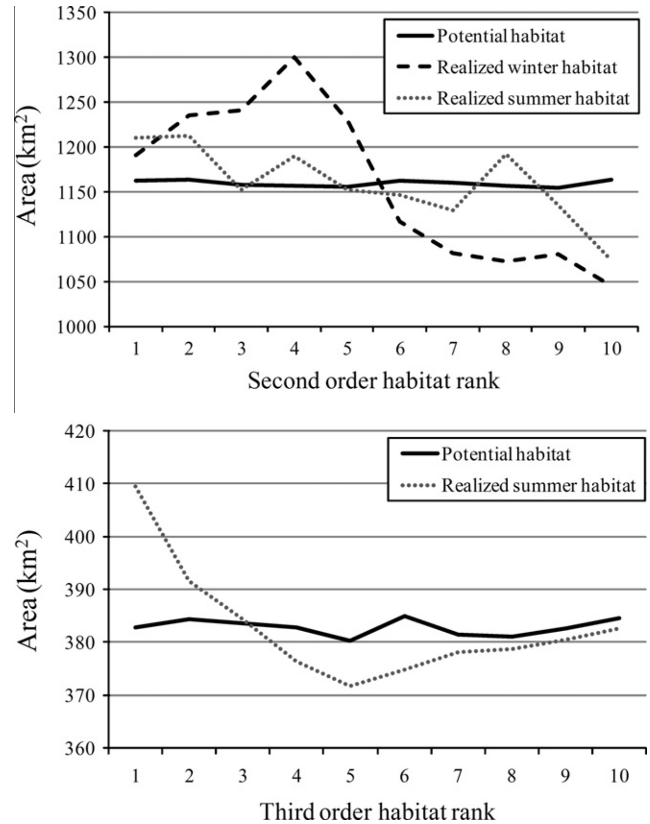

Fig. 3. Indirect habitat loss associated with the avoidance of human developments at the second-order and third-order scale for the Atlin northern mountain woodland caribou herd in northern British Columbia from 2000 to 2002. The difference between potential and realized habitat ranks 8–10 can be considered the amount of high quality habitat that was lost due to current human development (second-order: 276.2 km^2 in winter, 60.9 km^2 in summer; third-order: 6.4 km^2 in summer). Total study area size was 11,593.8 km^2 at the second-order and 3828 km^2 at third-order.

4. Discussion

This study builds on existing techniques that evaluate caribou avoidance of human development (e.g., Dyer et al., 2001; Johnson et al., 2005) and provides an innovative approach to quantify the amount and quality of indirect habitat loss by comparing estimates of potential and realized habitat. To model avoidance we first generated a biologically relevant cumulative ZOI that incorporated multifarious human developments into two-scale seasonal RSF models. The cumulative ZOI reduced model complexity and served as a simple tool to evaluate a large range of human development types as one unit. As we hypothesized, we found avoidance of the cumulative ZOI was strongest at the second-order (landscape) scale. This is likely because caribou selected habitat in a hierarchical fashion with increased sensitivity to human developments at coarser scales. In our study area, the significant avoidance of human developments at the second-order restricted avoidance at the third-order because caribou could likely only maintain individual home ranges in areas far from human developments (Faille et

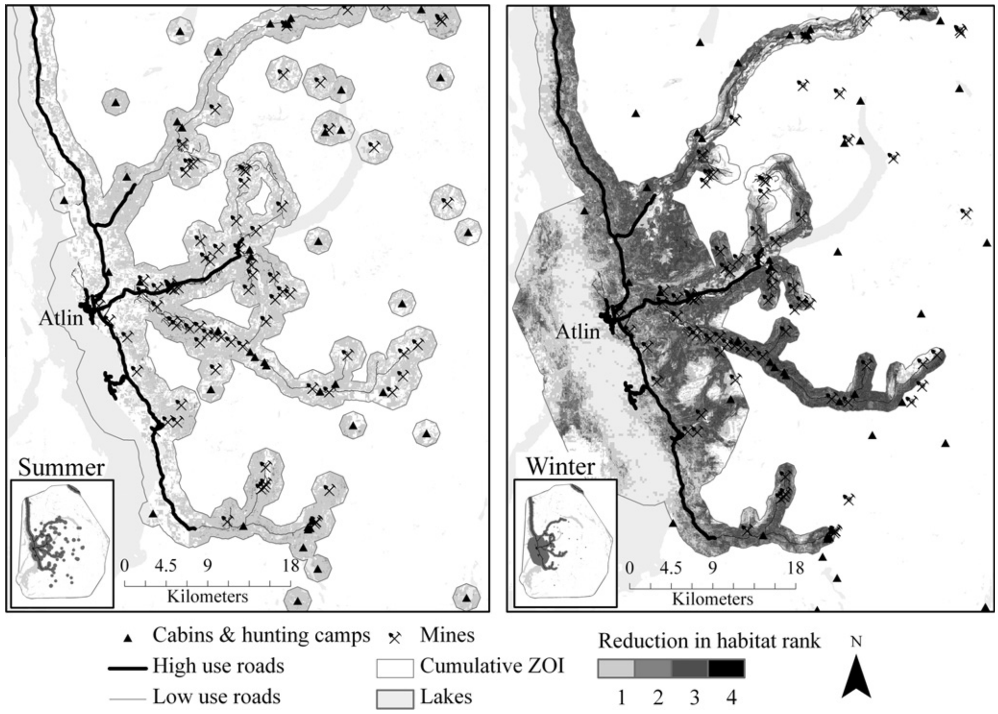

Fig. 4. Example of the reduction in habitat ranks between second-order potential and realized habitat in summer (left) and winter (right) for a portion of the study area surrounding the town of Atlin. Selection was measured for the Atlin northern mountain woodland caribou herd in northern British Columbia 2000 to 2002. Shading indicates the loss of 1–4 habitat ranks in each cell. The reduction in rank was used to determine the area (km^2) in each habitat rank category that was lost due avoidance of the cumulative zone of influence (ZOI) for each season.

al., 2010). Other studies have also demonstrated that woodland caribou avoid predation risk, the factor with the greatest potential to limit survival and fitness, at large scales (Gustine et al., 2006; Johnson et al., 2001; Rettie and Messier, 2000).

We were unable to test which limiting factors were responsible for avoidance, but the consistent avoidance of roads across seasons may be due to increased predation risk (by human and non-human predators) on roads where, for example, wolves may be more efficient predators (James and Stuart-Smith, 2000). Negative behavioral reactions that vary from increased vigilance to panicked flight have been observed for caribou following human-related harassment, low altitude aircraft and snowmobile traffic (Reimers and Colman, 2006; Seip et al., 2007). While these reactions may not result in large scale demographic consequences, they may increase perception of risk near infrastructure that results in avoidance. Avoidance has the potential to influence individuals' ability to obtain forage or circumvent harsh snow conditions and thus make caribou more vulnerable to predation (Dyer et al., 2001; James and Stuart-Smith, 2000).

We found that caribou avoidance of human developments varied between seasons and development types. In winter, caribou avoided the town of Atlin by 9 km, which is similar to avoidance of infrastructure found in habitat selection studies of reindeer (*Rangifer tarandus tarandus*) in Norway. At large spatial scales, Nellemann et al. (2001, 2003) found that reindeer avoided areas within 4–5 km of resorts, roads, power lines and a hydroelectric reservoir. Strong avoidance of human developments during winter is important because it can exacerbate the already high energetic costs associated with movement in snow, poor winter nutrition and female gestation (Parker et al., 2009). Since human activity on the landscape is low during winter, avoidance may occur in response to infrastructure alone (Vistnes and Nellemann, 2001). While we found that caribou avoided roads similarly across seasons, the ZOI around mines and cabins and hunting camps was much larger during summer. This avoidance corresponds to an increase in the level of human activity on the landscape due to active mines and ease of access to the road and ATV networks.

Divergent severity of avoidance buffers reported in the scientific literature may be a result of biological variance observed between populations, but could also be due to methodological inconsistency. For example, studies have used aerial surveys to measure caribou density in different seasons around mine sites (4 km, Weir et al., 2007), lichen height as an indirect indicator of reindeer grazing pressure and avoidance of roads (8 km, Dahle et al., 2008), proportions of caribou locations near seismic lines and oil well sites (0.25 km seismic lines, 1 km oil well sites, Dyer et al., 2001) and caribou use of areas around clearcuts before and after cutting occurred (15 km, Chubbs et al., 1993). The growing reliance on radio-telemetry in habitat studies and the widespread use of RSF models makes empirically driven buffer distances very appealing. However, models are limited in their ability to explicitly test the influence of individual developments on avoidance distances in areas that contain more than one development type. The spatial correlation of human developments on the landscape can make determining independent buffer distances difficult. However, in our study area we found significant avoidance of low use roads, mines and camps in areas that were separate from other developments, which suggests that these developments affect caribou habitat selection independently. Alternatively, because high use roads occurred predominately within the town of Atlin buffer in both seasons, it is likely that these two buffers are correlated. Thus, merging the individual avoidance distances into a cumulative ZOI buffer is appropriate since the exact underlying drivers of avoidance are difficult to separate in areas of aggregated developments. Further, the significant avoidance of the cumulative ZOI in both seasons supports the utility of our analysis to provide a consistent statistical approach that could be used to generate avoidance buffers across studies in the future.

Furthermore, the cumulative ZOI method limits the amount of habitat that is statistically affected by development to the area within the buffer (Fig. 4). In the Canadian high arctic, Johnson et al., (2005) compared the amount of caribou habitat lost due to avoidance of human development using ZOI buffers based on published literature and coefficients of 'distance to' development. Their ZOI analysis predicted that 6% of high quality habitat was avoided during the post-calving season, while disturbance coefficients of 'distance to' development predicted a 37% loss of high quality habitat. This latter result, based on quadratic functions, suggests that the effects of avoidance of human development were far reaching; up to 33 km from major developments. Similarly, quadratic functions indicated avoidance of up to 30 km from Atlin in our study area. However, we suggest that these results be interpreted with caution because quadratic functions may reflect landscape-level patterns in the availability of human development, and not necessarily avoidance per se. In the context of conflicting conservation/development priorities, we contend that an empirically derived cumulative ZOI is easily replicated and provides a consistent buffer that could be realistically implemented in management plans.

To examine the underlying quality of areas near human developments that were avoided by caribou, we statistically removed the cumulative ZOI from the realized RSF models to predict potential habitat (Hirzel and Le Ley, 2008). By spatially comparing the RSF predictions of potential and realized habitat we were able to examine how avoidance of human disturbance modified habitat quality. We found that 8% of high quality winter habitat and 2% of high quality summer habitat was degraded due to indirect avoidance of areas near human developments at the second-order (landscape) scale (Fig. 3). Our approach relied on the assumption that the probability of caribou occurrence is related to habitat quality. This may not be the case in areas where extensive habitat loss could mask true habitat preferences of sampled animals. In these situations, occurrence may not always be predictive of habitat quality (van Horne, 1983) because individuals may select risky habitats (attractive sinks) which decrease survival (Nielsen et al., 2006). Attractive sinks are common in human-altered habitats because species are unable to adapt to mortality risks that were absent in their evolutionary history (Schlaepfer et al., 2002). If this is the case, modeling the loss of high quality habitat may underestimate negative demographic consequences, resulting in biologically conservative ZOIs.

Recently, several studies have attempted to link habitat quality with survival (Nielsen et al., 2010) or abundance (Patthey et al., 2008). To estimate habitat selection of grizzly bears in Alberta, Canada, Nielsen et al. (2010) modeled potential habitat that accounted for growth and reproduction with food resource abundance and realized habitat that accounted for survival with regional mortality risk. By subtracting the realized habitat quality from the potential habitat quality they measured the habitat deficit, or the absolute habitat loss, and found that the greatest deficit occurred in low elevation forests with high human development and high food diversity (Nielsen et al., 2010). In the European Alps, Patthey et al. (2008) counted lekking male black grouse (*Tetrao tetrix*) along transects at ski resorts and natural sites. They found that abundance was approximately 36% lower in ski resort sites which suggests a large demographic effect of winter tourism on grouse abundance (Patthey et al., 2008). While both these approaches use novel methodological techniques linking demographic processes with habitat selection, they also rely on data that can be prohibitive to collect. The cost associated with measuring demographic parameters can be a strong limitation in many study systems; especially in northern regions where scientific capacity may be low but where conservation actions have the potential to protect at risk populations before large-scale habitat alteration occurs. However, inferring important links between habitat quality and fitness will improve our ability to predict the effects of indirect avoidance of habitat on affected populations.

The results of our RSF models confirm many habitat relationships found in previous studies. In winter, at the second-order scale, we found that caribou in the Atlin herd selected lodgepole pine/lichen complexes, spruce/fir and mid-elevations; all of which are typical of northern mountain populations (Florkiewicz et al., 2007; Gustine and Parker, 2008; Poole et al., 2000). In our study area, low elevation lodgepole pine forests were also often the sites for roads and towns and thus avoidance of these developments forced a trade-off resulting in the loss of limited high quality habitat. The winter potential habitat map revealed that the areas surrounding the town of Atlin and high use roads contained high quality habitat that was used less than expected. However, use of resources by northern caribou populations varies extensively among regions, and local responses to habitat variables, winter weather conditions and human developments may differ from results specific to the Atlin herd. For example, some northern mountain populations are known to select dry pine/lichen forests in the winter (Florkiewicz et al., 2007; Gustine and Parker, 2008) while others avoid pine stands (Gustine et al., 2006). The relatively lower predictive ability of the third-order winter RSF models may reflect a mismatch between the resolution of the available predictor covariates and the scale of selection measured (Boyce, 2006). Fine scale variation in snow conditions, for example, may influence caribou habitat selection and could affect avoidance of the ZOI.

During summer at both scales, caribou selected alpine habitats, which is likely a result of selection for new high quality forage and relief from insect harassment (Ion and Kershaw, 1989). Forage quality (nitrogen content) has been correlated with snowmelt gradients in Sweden at multiple spatial scales (Mårell et al., 2006). This may explain summer selection for areas that had high percent snow cover during the previous winter and suggests that selection for forage quality is important during summer at both spatial scales. Overall, high quality summer habitat was not impacted by indirect avoidance as intensely as winter habitat, likely because caribou selected for high elevations where conflict with human development is less severe. However, it is well established that caribou and reindeer tend to be most sensitive to development during the calving period (Vistnes and Nellemann, 2001), which was included in our summer season. Thus, human development close to calving areas could have significant consequences on populations. Our study was intended to examine large scale habitat selection patterns in relation to human infrastructure and we did not specifically analyze fine scale avoidance during calving. However, exploratory analyses of selection during the month of June revealed that caribou selected higher elevations and alpine and krummholz landcovers, but showed no significant difference in avoidance of the human ZOI buffer (June $\beta = -0.633$ SE = 0.178 vs. summer $\beta = -0.478$ SE = 0.061). Therefore, in our study area, habitat selection during calving does not appear to be influenced to a greater extent by human development than the entire summer period.

5. Conclusion

Given the widespread avoidance of human developments by caribou as well as the growing industrial development and the predicted effects of climate change in northern ecosystems (Pereira et al., 2010), new tools to quantitatively study the effects of direct and indirect loss of caribou habitat are required. The tendency for development to proceed in small increments can make understanding the cumulative impacts of multiple development across space and time difficult (Gunn et al., 2011; Sorensen et al., 2008). While the cumulative impact of human development types in our study area may seem minor compared to the severe threats facing southern woodland caribou herds, our approach to estimating indirect habitat loss has the potential to identify the underlying habitat quality in areas that are avoided and thus, quantifying the impact of past habitat alterations on selection – an important consideration when evaluating cumulative effects (Krausman, 2011). Dynamic temporal and spatial comparisons between potential and realized habitat could promote sustainable management by identifying high quality habitat in areas close to human developments. These areas may be important for population persistence because degraded habitat in close proximity to infrastructure could provide important restoration or mitigation opportunities (Nellemann et al., 2010). While the mechanisms driving caribou avoidance of human developments merits further study, habitat selection studies can provide an efficient way to monitor indirect habitat loss and proactively promote conservation before large-scale population impacts occur (Patthey et al., 2008). Finally, understanding the effects of multiple development types on habitat selection can facilitate the development of dynamic models that can be used to predict the potential impacts of future developments (Gunn et al., 2011; Nielsen et al., 2010).

Acknowledgements

We acknowledge the Taku River Tlingit First Nation, whose commitment to sustainable management of the wildlife and resources identified the need for and supported this project through its entirety. Special thanks to Taku River Tlingit members Jerry Jack and Phil Tizya for valuable field work. We thank Round River staff who assisted with field work and habitat modeling, especially Rick Tingey for GIS assistance. Our collaborators at the University of Calgary, Greg McDermid and Adam McLane, assisted with the development of a landcover classification. The manuscript benefited from the revisions of Michael Mitchell, Paul Krausman, Claire Polfus and four anonymous reviewers. Final thanks to the British Columbia Ministry of Environment for providing animal location data, especially Karen Diemert and Norm Maclean. Funding was provided by the Habitat Stewardship Program for Species at Risk of Environment Canada, the Taku River Tlingit First Nation, Round River Conservation Studies and the University of Montana.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.07.023.

References

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., Matthiopoulos, J., 2008. Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31, 140–160.

Alldredge, J.R., Thomas, D.L., McDonald, L.L., 1998. Survey and comparison of methods for study of resource selection. Journal of Agricultural Biological and Environmental Statistics 3, 237–253.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24, 127–135.

Boyce, M.S., 2006. Scale for resource selection functions. Diversity and Distributions 12, 269–276.

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecological Modelling 157, 281–300.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., Hilton-Taylor, C., 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16, 909–923.

Chubbs, T.E., Keith, L.B., Mahoney, S.P., McGrath, M.J., 1993. Responses of woodland caribou (*Rangifer tarandus caribou*) to clear-cutting in east-central Newfoundland. Canadian Journal of Zoology 71, 487–493.

Compton, B.W., Rhymer, J.M., McCollough, M., 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology 83, 833–843.

COSEWIC, 2002. COSEWIC assessment and update status report on the woodland caribou, *Rangifer tarandus caribou*, in Canada. In: Thomas, C.D., Gray, D.W. (Eds.), Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ontario, Canada, xi + 98 pp.

Dahle, B., Reimers, E., Colman, J.E., 2008. Reindeer (*Rangifer tarandus*) avoidance of a highway as revealed by lichen measurements. European Journal of Wildlife Research 54, 27–35.

Duchesne, T., Fortin, D., Courbin, N., 2010. Mixed conditional logistic regression for habitat selection studies. Journal of Animal Ecology 79, 548–555.

Dyer, S.J., O'Neill, J.P., Wasel, S.M., Boutin, S., 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management 65, 531–542.

Dyer, S.J., O'Neill, J.P., Wasel, S.M., Boutin, S., 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Canadian Journal of Zoology 80, 839–845.

Faille, G., Dussault, C., Ouellet, J.P., Fortin, D., Courtois, R., St-Laurent, M.H., 2010. Range fidelity: the missing link between caribou decline and habitat alteration? Biological Conservation 143, 2840–2850.

Florkiewicz, R., Maraj, R., Hegel, T., Waterreus, M., 2007. The effects of human land use on the winter habitat of the recovering Carcross woodland caribou herd in suburban Yukon Territory, Canada. Rangifer Special Issue 17, 181–197.

Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H.M., Stenhouse, G.B., Beyer, H.L., 2004. Removing GPS collar bias in habitat selection studies. Journal of Applied Ecology 41, 201–212.

Frair, J.L., Merrill, E.H., Beyer, H.L., Morales, J.M., 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. Journal of Applied Ecology 45, 1504–1513.

Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E., Jerde, C.L., 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75, 887–898.

Gunn, A., Johnson, C.J., Nishi, J.S., Daniel, C.J., Russell, D.E., Carlson, M., Adamczewski, J.Z., 2011. Understanding the cumulative effects of human activities on barren-ground caribou. In: Krausman, P.R., Harris, L.K. (Eds.), Cumulative Effects in Wildlife Management: Impact Mitigation. CRC Press, Boca Raton, FL, pp. 113–134.

Gustine, D.D., Parker, K.L., 2008. Variation in the seasonal selection of resources by woodland caribou in northern British Columbia. Canadian Journal of Zoology 86, 812–825.

Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P., Heard, D.C., 2006. Interpreting resource selection at different scales for woodland caribou in winter. Journal of Wildlife Management 70, 1601–1614.

Hall, D.K., Riggs, G.A., Salomonson, V.V., 2000. MODIS/Terra Snow cover 8-day L3. Global 500 m Grid V03, February 2000 to February 2002. National Snow and Ice Data Center. Digital media, Boulder, CO, USA.

Hastie, T.J., Tibshirani, R., 1990. Generalized Additive Models. Chapman and Hall, London.

Hegel, T.M., Mysterud, A., Ergon, T., Loe, L.E., Huettmann, F., Stenseth, N.C., 2010. Seasonal effects of Pacific-based climate on recruitment in a predator-limited large herbivore. Journal of Animal Ecology 79, 471–482.

Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R., Macdonald, D., 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. Journal of Animal Ecology 74, 455–463.

Hirzel, A.H., Le Ley, G., 2008. Habitat suitability modelling and niche theory. Journal of Applied Ecology 45, 1372–1381.

Hosmer, D.W., Lemeshow, S. (Eds.), 2000. Applied Logistic Regression. John Wiley and Sons, New York, New York, USA.

Houle, M., Fortin, D., Dussault, C., Courtois, R., Ouellet, J.P., 2010. Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest. Landscape Ecology 25, 419–433.

Ion, P.G., Kershaw, G.P., 1989. The selection of snow patches as relief habitat by woodland caribou (*Rangifer tarandus caribou*), Macmillan Pass, Selwyn/Mackenzie Mountains, NWT, Canada. Arctic and Alpine Research 21, 203–211.

James, A.R.C., Stuart-Smith, A.K., 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management 64, 154–159.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.

Johnson, C.J., Nielsen, S.E., Merrill, E.H., McDonald, T.L., Boyce, M.S., 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70, 347–357.

Johnson, C.J., Parker, K.L., Heard, D.C., 2000. Feeding site selection by woodland caribou in north-central British Columbia. Rangifer, 159–172.

Johnson, C.J., Parker, K.L., Heard, D.C., 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia 127, 590–602.

Johnson, C.J., Boyce, M.S., Case, R.L., Cluff, H.D., Gau, R.J., Gunn, A., Mulders, R., 2005. Cumulative effects of human developments on arctic wildlife. Wildlife Monographs 160, 1–36.

Joly, K., Nellemann, C., Vistnes, I., 2006. A reevaluation of caribou distribution near an oilfield road on Alaska's North Slope. Wildlife Society Bulletin 34, 866–869.

Keating, K.A., Cherry, S., 2004. Use and interpretation of logistic regression in habitat selection studies. Journal of Wildlife Management 68, 774–789.

Koper, N., Manseau, M., 2009. Generalized estimating equations and generalized linear mixed-effects models for modelling resource selection. Journal of Applied Ecology 46, 590–599.

Krausman, P.R., 2011. Quantifying cumulative effects. In: Krausman, P.R., Harris, L.K. (Eds.), Cumulative Effects in Wildlife Management: Impact Mitigation. CRC Press, Boca Raton, FL, pp. 47–64.

MacKinnnon, A., Pojar, J., Coupe, R. (Eds.), 1999. Plants of Northern British Columbia, second ed.. Lone Pine Publishing, Vancouver, BC.

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

Mårell, A., Hofgaard, A., Danell, K., 2006. Nutrient dynamics of reindeer forage species along snowmelt gradients at different ecological scales. Basic and Applied Ecology 7, 13–30.

Nellemann, C., Vistnes, I., Jordhoy, P., Strand, O., 2001. Winter distribution of wild reindeer in relation to power lines, roads and resorts. Biological Conservation 101, 351–360.

Nellemann, C., Vistnes, I., Jordhoy, P., Strand, O., Newton, A., 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. Biological Conservation 113, 307–317.

Nellemann, C., Vistnes, I., Jordhoy, P., Stoen, O.G., Kaltenborn, B.P., Hanssen, F., Helgesen, R., 2010. Effects of recreational cabins, trails and their removal for restoration of reindeer winter ranges. Restoration Ecology 18, 873–881.

Nielsen, S.E., Stenhouse, G.B., Boyce, M.S., 2006. A habitat-based framework for grizzly bear conservation in Alberta. Biological Conservation 130, 217–229.

Nielsen, S.E., McDermid, G., Stenhouse, G.B., Boyce, M.S., 2010. Dynamic wildlife habitat models: seasonal foods and mortality risk predict occupancy-abundance and habitat selection in grizzly bears. Biological Conservation 143, 1623–1634.

Oosenbrug, S.M., Theberge, J.B., 1980. Altitudinal movements and summer habitat preferences of woodland caribou in the Kluane Ranges, Yukon-Territory. Arctic 33, 59–72.

Parker, K.L., Barboza, P.S., Gillingham, M.P., 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23, 57–69.

Patthey, P., Wirthner, S., Signorell, N., Arlettaz, R., 2008. Impact of outdoor winter sports on the abundance of a key indicator species of alpine ecosystems. Journal of Applied Ecology 45, 1704–1711.

Pereira, H.M., Leadley, P.W., Proenca, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarres, J.F., Araujo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guenette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for global biodiversity in the 21st century. Science 330, 1496–1501.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J., Stenseth, N.C., 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20, 503–510.

Poole, K.G., Heard, D.C., Mowat, G., 2000. Habitat use by woodland caribou near Takla Lake in central British Columbia. Canadian Journal of Zoology 78, 1552–1561.

Railsback, S.F., Stauffer, H.B., Harvey, B.C., 2003. What can habitat preference models tell us? Tests using a virtual trout population. Ecological Applications 13, 1580–1594.

Reimers, E., Colman, J.E., 2006. Reindeer and caribou (*Rangifer tarandus*) response towards human activities. Rangifer 26, 55–71.

Rettie, W.J., Messier, F., 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23, 466–478.

Rodgers, A.R., Carr, A.P., 2002. Home Range Extension. Ontario Ministry of Natural Resources' Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Schlaepfer, M.A., Runge, M.C., Sherman, P.W., 2002. Ecological and evolutionary traps. Trends in Ecology & Evolution 17, 474–480.

Seip, D.R., Johnson, C.J., Watts, G.S., 2007. Displacement of mountain caribou from winter habitat by snowmobiles. Journal of Wildlife Management 71, 1539–1544.

Soberón, J., 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters 10, 1–9.

Sorensen, T., McLoughlin, P.D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., Boutin, S., 2008. Determining sustainable levels of cumulative effects for boreal caribou. Journal of Wildlife Management 72, 900–905.

StataCorp, 2007. Stata Statistical Software: Release 11. StataCorp LP, College Station, Texas.

UNEP, 2001. In: Nellemann, C., Kurllerud, L., Vistnes, I., Forbes, B.C., Kofinas, G., Kaltenborn, B.P., Gron, O., Henry, D., Magomedova, M., Lambrechts, C., Larsen, T.S., Schei, P.J., Bobiwash, R. (Eds.), GLOBIO – Global Methodology for Mapping Human Impacts on the Biosphere. United Nations Environmental Programme, Nairobi, Kenya.

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

Vistnes, I., Nellemann, C., 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. Journal of Wildlife Management 65, 915–925.

Vistnes, I., Nellemann, C., 2008. The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. Polar Biology 31, 399–407.

Vistnes, I., Nellemann, C., Jordhoy, P., Stoen, O.G., 2008. Summer distribution of wild reindeer in relation to human activity and insect stress. Polar Biology 31, 1307–1317.

Vors, L.S., Boyce, M.S., 2009. Global declines of caribou and reindeer. Global Change Biology 15, 2626–2633.

Weir, J.N., Mahoney, S.P., McLaren, B., Ferguson, S.H., 2007. Effects of mine development on woodland caribou *Rangifer tarandus* distribution. Wildlife Biology 13, 66–74.

Wolfe, S.A., Griffith, B., Wolfe, C.A.G., 2000. Response of reindeer and caribou to human activities. Polar Research 19, 63–73.