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Movement pathways and habitat selection by woodland caribou during spring migration

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Abstract: Woodland caribou (*Rangifer tarandus caribou*) are a threatened species throughout Canada. Special management is therefore required to ensure habitat needs are met, particularly because much of their current distribution is heavily influenced by resource extraction activities. Although winter habitat is thought to be limiting and is the primary focus of conservation efforts, maintaining connectivity between summer and winter ranges has received little attention. We used global positioning system data from an interprovincial, woodland caribou herd to define migratory movements on a relatively pristine range. Non-linear models indicated that caribou movement during migration was punctuated; caribou traveled for some distance (movement phase) followed by a pause (resting/foraging phase). We then developed resource selection functions (RSFs), using case-controlled logistic regression, to describe resting/foraging sites and movement sites, at the landscape scale. The RSFs indicated that caribou traveled through areas that were less rugged and closer to water than random and that resting/foraging sites were associated with older forests that have a greater component of pine, and are further from water than were random available locations. This approach to analyzing animal location data allowed us to identify two patterns of habitat selection (travel and foraging/resting) for caribou during the migratory period. Resultant models are important tools for land use planning to ensure that connectivity between caribou summer and winter ranges is maintained.

Key words: AIC, Alberta, British Columbia, GIS, habitat selection, mixed effects models, non-linear modeling, *Rangifer tarandus caribou*, resource selection functions, validation.

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Introduction

Woodland caribou (*Rangifer tarandus caribou*) populations are declining in west-central Alberta, and the species is classified as threatened in both Alberta and British Columbia, and is listed federally as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Factors recognized as threats to population persistence are habitat alteration and loss, climate change, and predation, although predation is often considered to be a proximate contributor to caribou declines (Thomas & Gray, 2002). Caribou have evolved in dynamic landscapes, and shift their ranges in response to forest succession (Schaefer & Pruitt, 1991; Thomas & Gray, 2002). However, current rates of landscape change associated with industrial activities (primarily logging) are high and extensive (Schneider, 2002) and caribou ranges are being compressed (Smith *et al.*, 2000), such that range shifting may no longer be a viable option. In some areas, increased industrial activities have resulted in the direct loss of habitat and the displacement from calving and foraging areas (c.f. Nellemann & Cameron, 1998). In addition, indirect threats exist due to increased predation risk as a result of increased predator (wolf; *Canis lupus*) access to caribou habitat (James & Stuart-Smith, 2000) and the disruption of antipredator strategies (Bergerud & Elliot, 1986; Bergerud & Page, 1987; Seip, 1991; Edmonds & Smith, 1991; Rettie & Messier, 1998; James *et al.*, 2004).

As industrial pressures on the landscape escalate, concerns over the maintenance of functional habitat and impacts on habitat connectivity increase. High

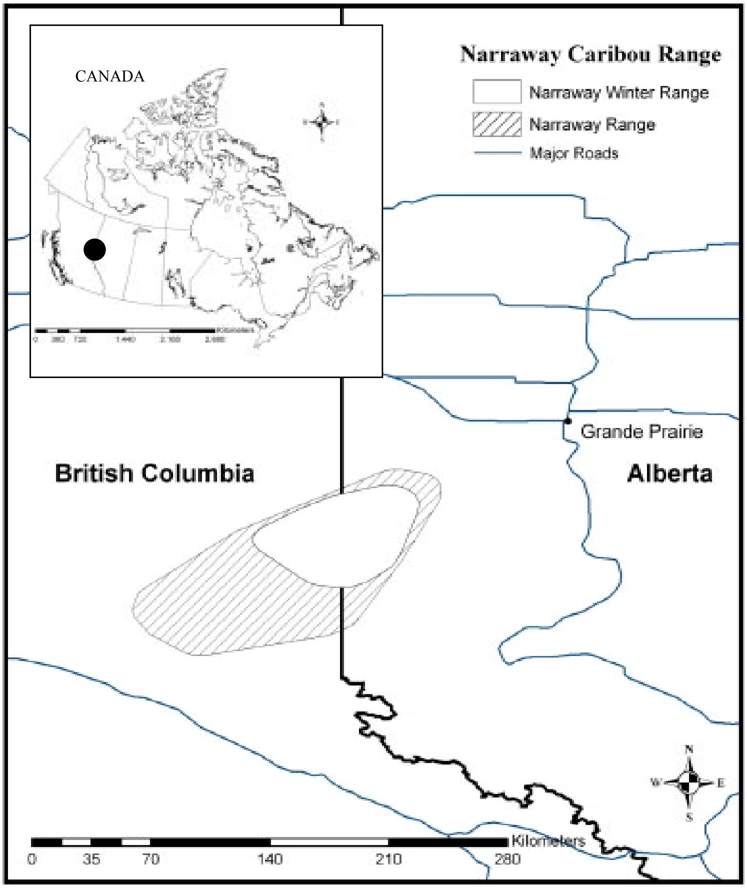

Fig. 1. The Narraway caribou range, located in west-central Alberta and east-central British Columbia, Canada.

habitat connectivity is necessary for caribou persistence on seasonal ranges (Seip, 1991; Rettie & Messier, 1998), and at a larger scale, for travel between summer and winter ranges. Migration can be defined in a number of ways; we adopted the operational definition of Berger (2004), which considers migration to be a "seasonal round-trip movement between discrete areas not used at other times of the year." Migration is typically associated with barren ground caribou (*Rangifer t. groenlandicus*), whose bi-annual migrations range between 800 and 5055 kilometers (Fancy *et al.*, 1988; Ferguson & Messier, 2000). However, some woodland caribou herds also migrate, albeit over shorter distances (56–300 kilometers; Fuller & Keith, 1981; Cumming & Beange, 1987; Edmonds, 1988). For both subspecies, migration may serve as an effective predator avoidance strategy, with caribou (prey) distancing themselves from predators (primarily wolves) whose movements are restricted during the denning period (Bergerud 1988; Fryxell & Sinclair, 1988).

Current industrial activities are limited to low elevation areas, potentially effecting caribou only during migration and while on the winter range. Considerable attention has focused on aspects of habitat use during the winter months. While the maintenance of winter range is clearly important, we also recognize the need to maintain connectivity between seasonal ranges. This is central to conservation efforts as woodland caribou display high fidelity to both summer and winter ranges (Schaefer *et al.*, 2000), and the availability of functional habitat outside current ranges is questionable, potentially limiting their ability to shift ranges.

Although the general characteristics of many migratory routes have been documented, little is known about caribou habitat use along these routes. We address this by assessing habitat use along migration routes for the Narraway caribou herd in west-central Alberta and east-central British Columbia. The Narraway is unique among caribou ranges in the region, as it has experienced only minor amounts of industrial development. This characteristic allowed us to model migration without the influence of anthropogenic disturbance. Through a combination of non-linear modeling and remote data collection, we developed habitat-based models identifying important coarse-scale attributes of the spring migration routes for the Narraway caribou herd. We validated these models using independent data from additional Narraway caribou. The specific objectives of this project were to 1) quantify the movement patterns of caribou in the Narraway range during the spring migratory period and 2) determine whether these patterns were associated with selection of particular habitat attributes.

Study area

Our efforts focused on woodland caribou using the Narraway range (*ca* 5000 km^2; Fig. 1), which is located approximately 130 kilometers southwest of Grande Prairie, Alberta, Canada, and extends across the Alberta–British Columbia provincial boundary. In British Columbia, this range is referred to as the Belcourt range. From a regional perspective, this range is unique in that it exists in a relatively pristine state. Most animals winter on a large plateau that spans the Alberta–British Columbia border, west of the Narraway River. Much of this area is poorly drained and dominated by black spruce (*Picea mariana*) and tamarack (*Larix laricina*). Within this central muskeg area are small patches of upland forest dominated by lodgepole pine (*Pinus contorta*) and black spruce. The winter range is under increasing development pressure from forestry and energy sectors. In the summer, the caribou move southwest into the mountains of British Columbia, near the headwaters of the Narraway and Fraser Rivers. While the summer range is not contained within a protected area, its alpine location currently discourages industrial development.

Methods and materials

Caribou location data

Adult female caribou using the Narraway range were captured using helicopter-based net gunning techniques. All capture and handling methods were approved by the University of Alberta, Faculty of Agriculture, Forestry and Home Economics Animal Care Committee (Protocol 2003-29D) and adhere to guidelines outlined by the Canadian Council on Animal Care. Caribou were outfitted with global positioning system (GPS) collars (Lotek GPS 1000 or Lotek GPS 2200, Lotek Engineering, Inc., Newmarket, Ontario, Canada.). Collars were programmed to acquire a fix on one of two schedules: a standard 2-hour schedule or a variable schedule in which locations were acquired every 30 minutes, two hours, or six hours, depending on the day of the week. While we acknowledge the existence of autocorrelation within the data set, we were interested in selection occurring throughout the entire process of migration and therefore chose not to rarify the data. Use of case-controlled logistic regression (see Selection Analysis) reduced the effect of autocorrelation on resultant relationships. All locations with horizontal dilution of precision (HDOP) values greater than 12, indicating poor location accuracy, were removed prior to analysis. Models were developed using the migration patterns of eight caribou across two years (2002–2003; four different caribou each year). Data were pooled across years and individuals. For two caribou, we had data for multiple spring migration events. Because caribou tended to use the same route in all years, only the first event for which we had data was used in the analysis. All caribou moved independently of one another in time. Data from an additional six caribou were used for model validation.

We defined the start of migration on an individual basis, as three consecutive movements in a southwest direction outside the winter range (100% Minimum Convex Polygon for 1 Dec–30 Apr locations) of an animal. The last cluster of locations acquired prior to 15 June in any migration event was assumed to represent calving and was removed from the analysis.

Identification of scales of movement

Visual inspection of migration pathways indicated that caribou display punctuated movement during migration, whereby a pattern of traveling followed by a period of limited movement was repeated. In order to model what was visually apparent in the data, we used a nonlinear curve fitting procedure to identify scales of movement by individual caribou (Sibly *et al.*, 1990; Johnson *et al.*, 2002). Nonlinear modeling was carried out in SPSS 11.5 (SPSS, Inc.). This method approximates a traditional broken-stick model, allowing behaviors to be objectively split into bouts (Sibly *et al.*, 1990). Resting/foraging movements were assumed to be associated with lower movement rates relative to traveling movements. The nonlinear model takes the form:

$$y = \log_e\left(N_s \lambda_s e^{-\lambda_s r} + N_l \lambda_l e^{-\lambda_l r}\right) \quad [1]$$

where s and l refer to processes that are assumed to generate small (resting/foraging) and large scale (traveling) movements; y is the predicted number of movements that occur during each discrete interval of movement rates. N is the number of small and large scale movements that occur at each rate interval, r is the movement rate and λ represents the probability that an event, either resting/foraging or traveling, occurs in the next movement rate interval.

Following model fit, we used the estimated parameters (N, λ) to identify a scale criterion interval (r_C) that defines the break point between large and small-scale movements (Johnson *et al.*, 2002) and is calculated as follows:

$$r_c = \left(1/\lambda_s - \lambda_l\right) * \log_e\left(N_s \lambda_s / N_l \lambda_l\right) \quad [2]$$

Movement rates of caribou less than r_C were considered to be associated with resting/foraging and those greater than r_C were assumed to be associated with traveling.

We defined a patch by consecutive locations identified by the nonlinear modeling procedure to be small-scale movements (i.e., clusters of locations classified as resting/foraging). In order to capture the variation within a patch, we randomly selected three locations, separated by a minimum distance of 100 meters, within the patch for analysis. All patches and traveling locations were used in the analysis. If the last large-scale movement prior to the caribou entering a defined patch was a distance of less than the location interval multiplied by the scale criterion interval for that caribou, it was reclassified to a resting/foraging location.

Table 1. GIS predictor variables used to model habitat selection along the spring migratory pathways of woodland caribou using the Narraway caribou range in west-central Alberta and east-central British Columbia, Canada (2002–2003). All response variables were continuous.

Variable code	Name	GIS Data source
elev	Elevation (m)	Digital Elevation Model (DEM)[a]
TRI	Terrain Ruggedness Index	DEM spatial analyst calculation
Distwater[b]	Distance to Water (km)	Spatial Analyst calculation
Distedge[c]	Distance to Edge (km)	Spatial Analyst calculation
age	Stand Age (yr)	Forest cover layerd
age^2	Stand Age Quadratic (yr^2)	Calculated from forest cover layer
density	Canopy Cover (%)	Forest cover layer
spruce	% Spruce	Forest cover layer
pine	% Pine	Forest cover layer

[a] The DEM was obtained from the National Topographic Data Base.
[b] Distance to closest permanent water source.
[c] Distance to closest natural or anthropogenic edge. Natural edges included any non-forest classed polygon and forest polygons whose density was <10%, or whose age <30 years, or that had a deciduous component of >70%.
[d] Forest cover layers were provided by Weyerhaeuser Company (Alberta) and the British Columbia Ministry of Forests.

This reduced the risk of misclassification, as locations are classified as either small or large-scale movements based on the previous location.

Habitat attributes
Habitat attributes used in the modeling procedure were obtained from available forest cover and other spatial data (Table 1), within a Geographic Information System (GIS). A grid size of 30 meters was used for all environmental and forest cover data, accounting for the error associated with GPS collar locations (D'eon *et al.*, 2002). These data included distance, terrain, and habitat information. Slope, aspect and distances were calculated in the Spatial Analyst extension in ArcMap 8.3. We used a terrain ruggedness index (TRI) modified from Nellemann & Fry (1995) to account for local topographic variation. This was calculated using a 300-meter circular moving window and the formula: [3]

$$\text{TRI} = \frac{(\text{Aspect Variation} * \text{Mean Slope}) / (\text{Aspect Variation} + \text{Mean Slope})}{100}$$

When calculating distance to edge, we defined an edge as any polygon classified as non-forest (e.g., anthropogenic features, lakes, alpine habitat). If a polygon was classified as forest but had a stand density less than 10%; a stand age of less than 30 years, or had a deciduous component of greater than 70% it was also classed as an edge. We assumed that these forest classes would be recognized as different from the surrounding matrix by caribou.

We tested independent variables for collinearity using Pearson's correlation coefficient. When pairs of variables exhibited correlation values greater than |0.7|, we retained the variable that explained the most variation in the data, determined with a univariate logistic model. We tested all models for multicollinearity (Menard, 1995) using variance inflation factors (VIF). Multicollinearity was a concern if individual parameter VIF values were > 10 or if the mean VIF score for a given model was considerably larger than 1 (Chatterjee *et al.*, 2000). If models exhibited multicollinearity they were removed from the candidate set.

Modeling caribou migration
We conducted a preliminary logistic regression analysis to determine if habitat characteristics differed between resting/foraging sites and traveling sites, and to indicate whether modeling the behaviors independently was warranted.

Resource selection
To adequately describe the detected differences between resting/foraging and traveling sites, we chose to model each behavior separately. We used case-control logistic regression (Compton *et al.*, 2002) to estimate a discriminant function differentiating caribou use sites (either traveling or resting/foraging) from associated random locations. This discriminant function has been shown to be accurate in differentiating use from available locations (Manly *et al.*, 2002) and is equivalent to an RSF of the form exp ($\beta_1 x_1 + \ldots + \beta_p x_p$) (Manly *et al.*, 2002; Keating & Cherry, 2004). Used locations were compared against randomly generated available locations. Model structure followed the form:

$$w(\boldsymbol{x}) = \exp(\beta_1 x_{ij1} + \beta_2 x_{ij2} + \ldots \beta_K x_{ijK}) \quad [4]$$

where w(x) is the relative probability of use for the jth resource unit being selected at the ith choice for

Table 2. A priori candidate models used in assessing habitat selection during the migratory period on the Narraway caribou range in west-central Alberta and east-central British Columbia, Canada. Models were parameterized using caribou location data from the 2002 and 2003 spring migratory periods.

Model #	Model
1	Age + age^2 + distwater + distedge + pine + TRI
2	Distwater + age + age^2
3	Distwater
4	Pine + age + age^2
5	Spruce + age + age^2
6	TRI + age + age^2
7	Age + age^2
8	Pine + density
9	Spruce + density
10	Pine + distwater + density
11	TRI + density
12	TRI + distedge
13	TRI + distwater
14	TRI + Pine + Age +Age^2

the predictor variables, x_i, and the β_i's are the coefficient estimates for each predictor variable. Models were evaluated in the statistical package STATA 8.2 (Stata Corporation).

Fourteen candidate models were developed a priori, based on biologically relevant habitat attributes (Table 2). Model selection was based on AIC_c (Akaike's Information Criteria, corrected for small sample size bias; Anderson & Burnham, 2002), which balances model fit with model parsimony. Models were ranked based on the difference in the AIC_c values (ΔAIC_c), and Akaike weights (w_i) were used to assess the strength of evidence that any particular model was the best model in our set of candidate models (Anderson *et al.*, 2000). The ability of the models to accurately predict resting/foraging or traveling was determined through the validation process.

Selection analysis

We used case-controlled logistic regression to account for the spatial and temporal variation in habitats (Pendergast *et al.*, 1996), by defining availability based on each travel location or resting/foraging patch. Following Arthur *et al.* (1996), random locations were generated within a circle centered on the preceding use location with a radius either equal to the 95th percentile of the distance traveled for that location interval (30 min, 1 hr, 2 hr, 4 hr, 6 hr, 10 hr, 12 hr, and 18 hr) averaged across all animals or the distance between the two locations, whichever was larger. For locations identified as traveling by the non-linear modeling procedure, 20 random points were generated to represent available locations. Locations identified as resting/foraging required additional steps to replicate the clustered nature of the use locations. Twenty random points were generated as per traveling locations. We then buffered these points by the average area of all resting/foraging use areas (276 meter radius). Within this smaller buffer three random points were generated to compare against the three known use locations.

The locations of all random points, and hence available habitat, was limited to elevations less than 2000 meters and habitat classed as either a lake or river was excluded. Consistent with selection of use points within resting/foraging areas, random points were a minimum of 100 meters apart. Random point generation was carried out using Hawth's Analysis Tools extension (Version 2.0) in ArcGIS 8.3.

Spatial interpolation

The best model for each behavior was incorporated into a GIS framework (ArcGIS 8.3), and used to produce maps depicting a relative index of use for traveling and resting/foraging. Maps were area-adjusted, and relative index of use was assigned to 10 quantile bins, containing equal proportions.

Model validation

As our study design was based on used and available locations, model validation through Receiver Operating Characteristic (ROC) curves was inappropriate (Boyce *et al.*, 2002). However, we were able to use independent location data from an additional six caribou for model validation. We classified locations from each of these animals as either traveling or resting/foraging using the same non-linear modeling procedures used for classification of the locations used in model building (Table 5). The behavior-specific relative index maps, derived from the AIC-selected models, were then evaluated for their ability to predict use through a Spearman Rank Correlation, α = 0.05. Independent data points classified as traveling were used to assess the relative travel index surface, while those classified as resting/foraging were used to assess the relative index surface for resting/foraging. Strong correlations of the predicted map bins with independent validation data were taken to indicate good model fit and prediction. We use the term "index," rather than "probability" when referring to relative use, in response to recent criticisms from Keating & Cherry (2004) regarding estimation of probability surfaces from use-availability

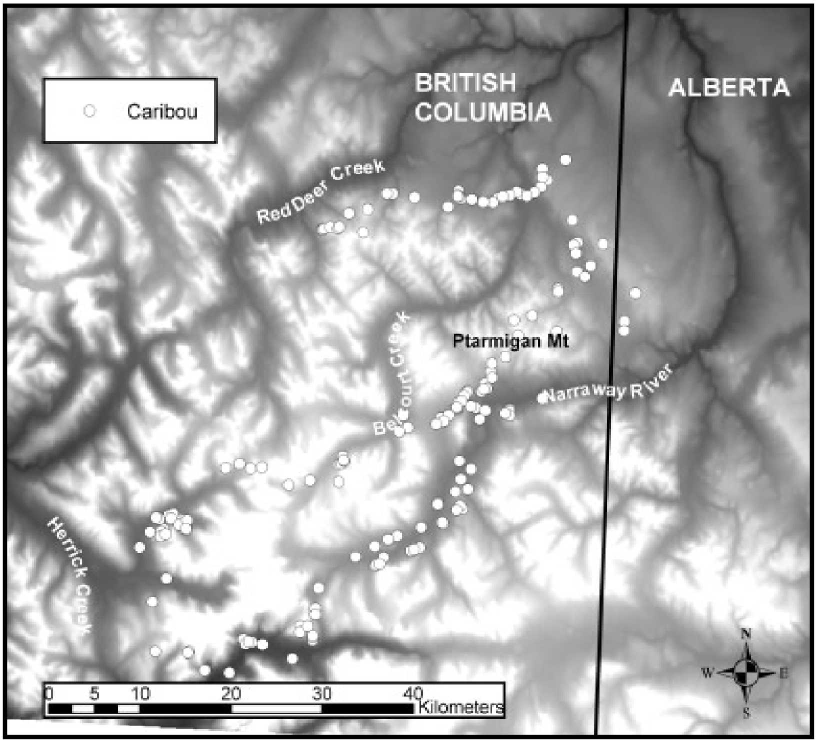

Fig. 2. General pathways taken during the spring migration (2002 & 2003) of collared Narraway caribou in west-central Alberta and east-central British Columbia, Canada.

designs. However, we note that their concerns were particularly acute in situations where higher order polynomials were being modeled, and our most complex models include only a quadratic term.

Results

Caribou relocations

The eight caribou used for model building followed one of two main routes (Fig. 2). While the general route traveled may be the same for multiple caribou included in the analysis, none were traveling together during the migratory period. Therefore, we assumed the decision to rest/forage or continue traveling was independent of the presence of other radiocollared caribou. Two caribou migrated through the northern part of the range using the Red Deer Creek area. A third animal used this area in 2003 but died early in migration and was excluded from the analysis. The remaining six caribou used the Narraway River region (Fig. 2; Table 3). Route selection varied more in this area than in the northern region, with some caribou traversing Ptarmigan Mountain before entering the Narraway Valley, while others went around. Variation was also apparent in the extent of travel in the Narraway River valley. Some caribou remained in this valley until they reached their calving grounds, while others branched off, using the Belcourt Creek drainage (Fig. 2; Table 3). The departure date from the winter range, overall distance traveled, and duration of migration also varied among caribou and year (Table 3).

Identification of scales of movement

Non-linear modeling identified the movement rate above which locations were classified as traveling and below which they were classified as resting/foraging (Table 4). The rate at which behaviors are differentiated is variable among individuals and migration strategies also appeared to vary among caribou with some traveling quickly and spending longer amounts of time at resting/foraging areas and while others traveled at a slower rate and spent less time in resting foraging areas. The migration strategy used and the collar schedule influenced the number of locations each animal contributed to the data set, such that the locations were not balanced across animals. Regardless of the strategy used, we assumed that caribou used similar habitats for each behavior.

Of the 176 caribou locations available for model building, 78 were identified as resting/foraging and 98 as traveling locations. The 78 resting/foraging locations represented 28 patches, thus the sample size for statistical analysis was 28 for resting/foraging models and 98 for traveling models (Table 5).

Modeling caribou migration

Discrimination was possible between habitat associated with resting/foraging and traveling sites, providing justification for modeling the behaviors separately. Resting/foraging locations were further from water and in less dense, older forests than were traveling locations.

Traveling

Of 14 candidate RSF models (Table 2), Model 13 was identified as the best model, indicating that travel loca-

Table 3. General characteristics of the spring migration (2001–2002) for collared woodland caribou using the Narraway range in west central Alberta and east-central British Columbia, Canada. The reported migration distance is the cumulative distance between the first identified migration location and the estimated calving location

Year	Caribou ID	Path	Migration distance (km)	Duration of migration (hr)	Departure date
Model building:					
2002	F709	Narraway	25.3	24	05/25/02
2002	F710	Red Deer Creek	27.5	40	05/27/02
2002	F711	Red Deer Creek	32.5	55	05/28/02
2002	F712	Narraway	73.1	300	06/03/02
2003	F715	Narraway via Ptarmigan	29.4	142	05/29/03
2003	F717	Narraway/Belcourt via Ptarmigan	70.1	116	05/22/03
2003	F722	Narraway/Belcourt via Ptarmigan	73.9	238	05/23/03
2003	F723	Narraway via Ptarmigan	119.1	206	05/16/03
		Mean ± SE	56.4 ± 11.8	140 ± 36	
Model validation:					
2001	F702	Narraway	145.2	360	05/11/01
2001	F704	Belcourt	33.2	75	05/06/01
2001	F705	Narraway/Belcourt	102.8	249	05/15/01
2002	F700	Narraway/Belcourt	76.8	246	05/29/02
2002	F708	Narraway via Ptarmigan	141.5	588	05/11/02
2003	F713	Red Deer Creek	64.9	308	05/11/03
		Mean ± SE	94.1 ± 18.1	304 ± 69	

Table 4. The rates (r_c) identified by non-linear modeling below which caribou locations from the Narraway Range in west-central Alberta and east-central British Columbia, Canada during the spring migratory period (2001 and 2003), were classified as resting/foraging and above which they were classed as traveling.

Model building			Model validation		
Year	Caribou ID	r_c (m/min)	Year	Caribou ID	r_c (m/min)
2002	F709	2.64	2001	F702	6.02
2002	F710	2.99	2001	F704	3.12
2002	F711	3.69	2001	F705	3.71
2002	F712	2.62	2002	F700	4.28
2003	F715	2.61	2002	F708	4.52
2003	F717	5.35	2003	F713	8.94
2003	F722	3.10			
2003	F723	9.81			
	Mean ± SE	4.10 ± 0.88		Mean ± SE	5.10 ± 0.87

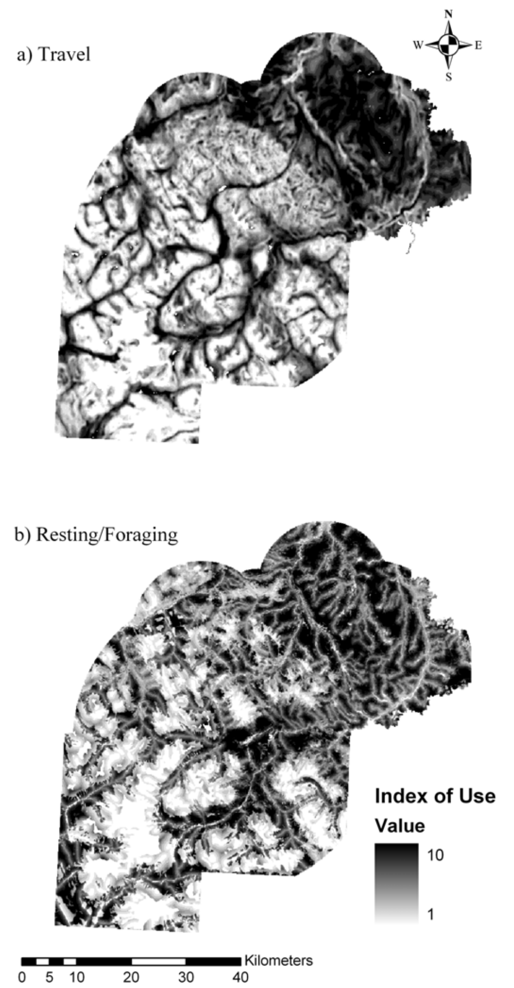

Fig. 3. Interpolated map surface showing the relative index of use during the spring migration on the Narraway caribou range in west-central Alberta and east-central British Columbia, Canada (2002 and 2003). The relative index of use for traveling is shown in (a) and that for resting/foraging in (b). Dark colors indicate a relatively high index value and light colors indicate a relatively low index value.

tions were more likely to be associated with less rugged terrain and were closer to water than were random available locations. The model takes the form:

$$\hat{w} = -8.921(TRI) - 0.375(distwater) \qquad [5]$$

The confidence intervals for TRI did not overlap zero, indicating that this variable had a stong influence on selection. The low Akiake weight associated with this model (0.423; Table 6), suggests only weak support that this model is the best predictive model, the second ranked model (Model 12) was also a 2-term model, and contained the TRI covariate, whose coefficient is consistent over both models. In addition, the second variable in Model 12, distedge, is a composite variable containing distwater, although it is not correlated with it. We were thus confident in selecting Model 13 as the top AIC model and incorporated it into a GIS framework identifying suitable traveling habitat for caribou (Fig. 3a).

Resting/foraging

Similarly, of the 14 candidate models evaluated for resting/foraging locations (Table 2), Model 14 was identified as the best model, indicating that resting/foraging locations were more likely to be associated with older, forests that have a greater component of pine, and were further from water than were random available locations. The model takes the form:

$$\hat{w} = 0.015(\boldsymbol{age}) - 0.00003(\text{age}^2) + 0.008(\boldsymbol{pine}) + 1.181(\boldsymbol{distwater}) \qquad [6]$$

The confidence intervals for the bolded covariates did not overlap zero, suggesting they had a strong influence on habitat selection. The Akiake weight associated with the global models was 0.633, indicating a moderate level of confidence that this model was the best of those considered, given the data (Table 7). We used this model to generate a GIS map indicating the occurrence of potential resting/foraging habitat for caribou during the spring migration (Fig. 3b).

Model validation

There was a significant positive correlation between the index surfaces and the occurrence of use locations from the independent data set (resting/foraging: $r_{(s)}$ = 0.697, P = 0.025; traveling $r_{(s)}$ = 0.636, P = 0.048). We interpreted this as evidence that the models were reasonably robust.

Discussion

In west-central Alberta, all caribou winter ranges fall under Forest Management Agreements, and are subject to timber harvest as well as increasing pressures from the oil and gas sectors. The identification of specific habitat attributes associated with caribou use is critical to the successful integration of caribou conservation strategies and sustainable land use management practices. Most attention has focused on the reduction of industrial effects on caribou winter ranges because these are

Table 5. Caribou locations used in the analysis of habitat selection along the spring migratory path of the Narraway Caribou Herd, west central Alberta and east-central British Columbia, Canada, 2001–2003. Resting/foraging and traveling movements were defined by non-linear modeling procedures.

Year	Caribou ID	# Patches	# Resting/Foraging locations	# Traveling locations	# Areas
Model building:					
2002	709	1	1	3	4
	710	2	6	17	19
	711	1	3	9	10
	712	4	11	7	11
Subtotal	4	**8**	**21**	**36**	**44**
2003	715	2	6	2	4
	717	4	10	10	14
	722	7	15	21	28
	723	7	21	29	36
Subtotal	4	**20**	**52**	**62**	**82**
Total	**8**	**28**	**73**	**98**	**126**
Model validation:					
2001	702	14	30	18	32
	704	4	10	4	8
	705	7	15	19	26
Subtotal	3	**25**	**55**	41	**66**
2002	700	8	22	6	14
	708	12	31	15	27
Subtotal	2	**20**	**53**	21	41
2003	713	3	9	3	6
Subtotal	1	**3**	**9**	**3**	**6**
Total	6	48	117	65	113

thought to be most limiting (Bjorge, 1984; Thomas *et al.*, 1996) and subject to the greatest development pressure (Hervieux *et al.*, 1996). However, as industrial activity expands, effects are reaching beyond the winter ranges and potentially influencing the use of traditional migration routes, and therefore affecting connectivity between summer and winter ranges.

Our study is the first attempt we are aware of to link observed movement patterns to habitat selection by woodland caribou during migratory events. We demonstrated that mountain caribou select certain habitat characteristics during migration and that this selection is dependent upon movement behavior, as inferred by the rate at which they are moving. When traveling, caribou select habitat that is closer to water and in less rugged terrain than random locations. This is consistent with least resistance theory (Hedenström, 2003), which hypothesizes animals will choose to travel in areas where they are able to move more quickly and expend less energy, typical of animals traveling between stopover sites. In a mountainous environment, these conditions are met along major drainages. When resting or foraging, caribou moved away from water bodies and into 'old' pine stands. These habitats are also consistent with migration theory, which suggests that stopover areas are used for refueling, resting and shelter (Hedenström, 2003) and occur in areas with relatively less predation risk (Berthold & Terrill, 1991). Although the analyses presented here do not address mechanisms, the general habitat attributes associated with these rates are consistent with those of higher forage (terrestrial lichen and forb) abundance (Pharo & Vitt, 2000). We associate risk of predation with distance to water, as wolves are known to travel along natural (Huggard, 1993) and anthropogenic (James, 1999) features at increased rates, thus increasing the likelihood of a predator–prey encounter (James, 1999; Dzus, 2001).

One of the primary hypotheses for migration by mountain caribou is separation from predators during the vulnerable calving period (Edmonds, 1988; Edmonds & Smith, 1991; Seip, 1991). Increased development on migratory routes connecting caribou summer and winter ranges could have two main effects. First, changes in predator abundance and distribution are likely (Dzus, 2001). As mature forests are replaced with younger forests post harvest, an increase in the abundance of other ungulate species is expected, which in turn will support larger populations of predator species (Seip & Cichowski, 1996;

Table 6. A comparison of habitat use models characterizing traveling locations of Narraway caribou during the spring migration (2002 & 2003). Models are ranked by ΔAIC_c values. Akaike weights (w_i) indicate the likelihood of the model. K indicates the number of parameters in the model.

Model #	K	AIC_c	ΔAIC_c	w_i	Rank
13	2	582.5943	0.000	0.423	1
12	2	583.0963	0.502	0.329	2
11	2	583.8423	1.248	0.227	3
1	6	589.0851	6.491	0.0164	4
3	1	593.1357	10.541	0.002	5
2	3	595.3133	12.719	<0.001	6
14	4	596.6661	14.072	<0.001	7
10	3	596.8473	14.253	<0.001	8
7	2	598.3683	15.774	<0.001	9
4	3	599.5813	16.987	<0.001	10
8	2	600.2523	17.658	<0.001	11
9	2	600.3663	17.772	<0.001	12
5	3	600.4973	17.903	<0.001	13
6	3	602.7233	20.129	<0.001	14

Table 7. A comparison of habitat use models characterizing resting/foraging locations of Narraway caribou during the spring migration (2002 & 2003). Models are ranked by ΔAIC_c values. Akaike weights (w_i) indicate the likelihood of the model. K indicates the number of parameters in the model.

Model #	K	AIC_c	ΔAIC_c	w_i	Rank
14	4	486.673	0.000	0.632989	1
2	3	488.000	1.327	0.326039	2
1	6	492.194	5.521	0.040046	3
4	3	501.284	14.611	0.000425	4
7	2	502.436	15.763	0.000239	5
5	3	503.038	16.365	0.000177	6
6	3	504.974	18.301	6.72E-05	7
13	2	508.356	21.683	1.24E-05	8
10	3	510.088	23.415	5.21E-06	9
3	1	516.158	29.485	2.51E-07	10
12	2	516.766	30.093	1.85E-07	11
9	2	519.402	32.729	4.95E-08	12
11	2	519.814	33.141	4.03E-08	13
8	2	519.954	33.281	3.75E-08	14

Rettie & Messier 1998; James & Stuart-Smith, 2000; Kunkel & Pletscher, 2000). Predator distribution may also be enhanced as they will gain access to previously remote areas through travel on anthropogenic linear features (Dzus, 2001), leading to increased encounter rates with and mortality rates for caribou (Seip, 1992; James, 1999; James & Stuart-Smith, 2000). Secondly, increased habitat alteration and fragmentation associated with industrial activity may lead to increased energetic costs, if caribou attempt to avoid these developments (Nellemann & Cameron, 1998; Dyer *et al.*, 2001; Vistnes & Nellemann, 2001). Migration is characteristically a balance between energetic outputs for locomotion and energetic inputs in the form of fuel intake (Hedenström, 2003). Detours are only possible when alternate areas for foraging exist and can be located without upsetting this balance (Alerstam, 2001; Hedenström, 2003). This has negative implications for long-term caribou persistence, as cows may arrive in the alpine in poor condition, effecting both the survival of the cow and her offspring. Ultimately, the cumulative effect of incremental development may result in the abandonment of migration routes all together (Alerstam *et al.*, 2003). If caribou stop migrating altogether, they may be exposed to higher predation risk year around if they stay on winter ranges, or they may stay in less productive alpine summer ranges.

The limited sample size available necessitated pooling data across years and individuals. We acknowledge that by pooling we may have masked individual variation in selection of habitats by caribou or variation due to changing environmental conditions across years. However, management cannot take place at the level of the individual or even on a yearly basis, in most cases. Global models may thus be most appropriate for management purposes, if they have been validated and shown to predict occurrence. Validation of the models is particularly important when, as in this case, the sampling design is unbalanced. Animals that are more prevalent in the data set, will contribute more information to the models, having a greater influence on the resulting selection coefficients. As our models adequately predicted the occurrence of independent caribou locations on the landscape we do not believe that any one animal from the model building set had undo influence on our models, and that our assumption that habitat selection is consistent across years and individuals was appropriate, at least within the confines of this study. Where sample sizes permit, individual models should be built to substantiate this assumption prior to pooling of data. Data collection over a greater number of years would better represent longer-term environmental variation, and resultant implications for habitat selection.

Migration is an important, and often neglected, component of the life history strategies of mountain caribou, and should be accounted for in conservation planning. The models produced here, while specific to the Narraway range in west-central Alberta, represent an important link between migratory behavior and habitat use. As a visual representation of these models, the maps allow for the identification of habitats selected during migration. These maps provide guidance for land use planners when evaluating management options.

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