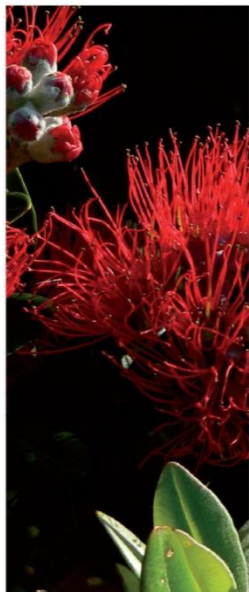


DISCLAIMER: PTAC does not warrant or make any representations or claims as to the validity, accuracy, currency, timeliness, completeness or otherwise of the information contained in this report , nor shall it be liable or responsible for any claim or damage, direct, indirect, special, consequential or otherwise arising out of the interpretation, use or reliance upon, authorized or unauthorized, of such information.

The material and information in this report are being made available only under the conditions set out herein. PTAC reserves rights to the intellectual property presented in this report, which includes, but is not limited to, our copyrights, trademarks and corporate logos. No material from this report may be copied, reproduced, republished, uploaded, posted, transmitted or distributed in any way, unless otherwise indicated on this report, except for your own personal or internal company use.



Use of anthropogenic linear features by alternative predators in woodland caribou range



Landcare Research
Manaaki Whenua

Use of anthropogenic linear features by alternative predators in woodland caribou range

A. David. M. Latham, M. Cecilia Latham

Landcare Research

Mark. S. Boyce, Stan Boutin

Department of Biological Sciences, University of Alberta

Prepared for:

Petroleum Technology Alliance Canada (PTAC)

Suite 400, 500 Fifth Ave. S. W.
Calgary, Alberta T2P 3L5
Canada

March 2013

*Landcare Research, Gerald Street, PO Box 40, Lincoln 7640, New Zealand, Ph +64 3 324 9999,
Fax +64 3 623 9998, www.landcareresearch.co.nz*

Reviewed by:

Approved for release by:

Jennyffer Cruz Bernal
Ecological Modeller Researcher
Landcare Research

Phil Cowan
Research Priority Area Leader
Invasive Species International

Landcare Research Contract Report:

LC 1224

Disclaimer

This report has been prepared by Landcare Research for Petroleum Technology Alliance Canada. If used by other parties, no warranty or representation is given as to its accuracy and no liability is accepted for loss or damage arising directly or indirectly from reliance on the information in it.



ISO 14001

© Petroleum Technology Alliance Canada 2013

This report has been prepared by Landcare Research New Zealand Limited for Petroleum Technology Alliance Canada and Landcare Research has agreed that Petroleum Technology Alliance Canada owns the copyright in the report. It may not be reproduced or copied, in whole or in part, in any form or by any means without the written permission of Petroleum Technology Alliance Canada.

Contents

Summary	v
1 Introduction.....	1
2 Background.....	1
3 Objective.....	3
4 Methods	3
4.1 Study area.....	3
4.2 Telemetry data	4
4.3 Statistical analysis.....	5
5 Results	8
5.1 Step selection analysis.....	8
5.2 Simulated versus observed movement paths	10
6 Discussion	11
7 Acknowledgements	13
8 References	14
9 Tables and Figures	19

Summary

Project and Client

- The assessment of anthropogenic linear features use by alternative predators in caribou range was conducted for the Petroleum Technology Alliance Canada by Landcare Research, Lincoln, between March 2012 and March 2013.

Objective

- Assess whether anthropogenic linear features influence coyote and black bear movements in woodland caribou range in northeastern Alberta, Canada.

Methods

- We used Global Positioning Systems (GPS) data from nine coyotes radiocollared between January 2006 and March 2007 in the West Side of the Athabasca River caribou range, Alberta, Canada.
- We used GPS data from 16 black bears radiocollared between 2001 and 2003 in the Cold Lake Air Weapons caribou range, Alberta, Canada.
- We used step selection functions (SSF) and compared observed to simulated animal movement paths to assess coyote and black bear selection and use of anthropogenic (all-season roads, pipelines right-of-way, and seismic lines) and natural linear features (minor rivers/streams and major rivers) as movement corridors.

Results

- Coyote movement was influenced by natural linear features (rivers and streams) throughout the year, possibly because they provide ease of travel during snow months and high abundance of prey in snow-free months.
- Coyote movement was further influenced by anthropogenic linear features, but use of these features differed depending on the type of line and season. Coyotes used and selected all-season roads and pipelines, especially during snow-free months, because of the high abundance of small prey and possibly as a refuge from harassment by wolves.
- Black bears showed strong selection for all anthropogenic linear-feature types during all seasons analyzed, likely because of the abundance of high-quality forage.

Conclusions

- Use of anthropogenic linear features as movement corridors might result in predators hunting in or close to caribou-preferred habitats (bogs and fens) more frequently than they did historically. If so, predator use of these features might increase predation risk for caribou close to them, resulting in functional loss of otherwise suitable habitat for caribou and increased incidental predation.

1 Introduction

The assessment of anthropogenic linear features use by alternative predators in caribou range was conducted for the Petroleum Technology Alliance Canada by Landcare Research, Lincoln, between March 2012 and March 2013.

2 Background

The boreal ecotype of woodland caribou (*Rangifer tarandus caribou*) is listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002) and under the federal Species at Risk Act (SARA) (Environment Canada 2008). In northeastern Alberta, Canada, caribou have been extirpated from about 60% of their historical range (Hummel & Ray 2008) and all currently monitored herds have shown declines in recent years (Schneider et al. 2010). Although a number of factors have been implicated in these population declines, predation has been identified as the primary proximate factor in Alberta (McLoughlin et al. 2003; Latham et al. 2011a) as well as in other jurisdictions (Boertje et al. 1996; Hayes et al. 2003; Wittmer et al. 2005). Wolves (*Canis lupus*) are believed to be responsible for most adult female mortality (ASRD & ACA 2010; McLoughlin et al. 2003; Latham 2009). However, populations have declined not only because of low adult female survival but also low calf survival and subsequent low recruitment to the population (ASRD & ACA 2010). Although wolves are likely contributing to low survival of caribou calves, grizzly bears (*Ursus arctos*), black bears (*U. americanus*), coyotes (*C. latrans*), and wolverine (*Gulo gulo*) also are believed to be important predators of calves (Ballard 1994; Crête & Desrosiers 1995; ASRD & ACA 2010).

Coyotes were historically absent from non-prairie Alberta; however, they have expanded north and west to include most of the mountainous and northern boreal forest of the province (Bowen 1981; Fuller & Keith 1981; Latham & Latham 2011). Although this new predator in the boreal forest could directly and indirectly impact a wide variety of prey and predator species, their ecology in this ecosystem is poorly understood. A recent study in northeastern Alberta by Latham et al. (in review) found that most coyotes showed positive selection for peatland-type habitats preferred by caribou during the calving season and also a small proportion of caribou calf in coyote diet, suggesting that although caribou are not important prey for coyotes they are incidental prey. However, evidence from eastern Canada suggests that invading coyotes can be effective predators of caribou, negatively affecting recruitment and population viability (Crête & Desrosiers 1995; Fournier & Faubert 2001).

In the boreal forest, black bears prey on calves of caribou (Mahoney et al. 1990; Seip 1991; Ballard 1994; Pinard et al. 2012), elk (*Cervus elaphus*) (Schlegel 1976), and moose (*Alces alces*) (Franzmann et al. 1980; Nolan & Barrett 1985), as well as fawns of white-tailed deer (*Odocoileus virginianus*; Kunkel & Mech 1994). In eastern Canada, Pinard et al. (2012) found that $\geq 50\%$ of caribou calf mortality could be attributed to predation by black bears. In northeastern Alberta, Latham et al. (2011b) showed that habitat selection by individual black bears in caribou range was highly variable, with approximately one-third of bears showing positive selection for habitats similar to those selected by caribou.

This suggests that bears that specialize on foraging in caribou-preferred habitats might contribute to high caribou calf mortality in these areas.

Historically, woodland caribou were provided with a partial refuge from predation by occupying old-growth forests or peatlands that are low-quality habitats for other ungulate species such as moose, and thus have few prey for predators dependent on ungulate prey (Bergerud et al. 1984). However, recent intensive activity by industry in and around caribou ranges may have affected the spatial separation strategy used by caribou to decrease the risk of predation (Bergerud 1974; Cumming 1992; James et al. 2004). In the boreal forest of northern Alberta linear developments are associated primarily with forestry and energy sector exploration and resource extraction (Schneider 2002). Industrial development in this area increased markedly during the mid-1990s, resulting in an average of 1.8 km/km² of all-season roads, pipeline-right-of-ways, and seismic exploration lines per township (10 × 10 km land survey units; Schneider 2002). Linear features constitute < 1.5% of the total land area, yet they are believed to have important implications for predator–woodland caribou dynamics in the region (James & Stuart-Smith 2000; COSEWIC 2002; Environment Canada 2008).

James (1999) and James and Stuart-Smith (2000) hypothesized that industrial linear features increased hunting efficiency by wolves (and possibly other predators) in caribou ranges. For example, linear features might increase visual encounters with caribou by enhancing wolf line-of-sight, increase wolf olfactory encounters with fresh caribou trails, increase wolf travel speeds through peatlands or alter the orientation of wolf movements to include a greater proportion of caribou habitat in hunting forays (Latham 2009). Further, Latham et al. (2011c) showed that anthropogenic linear features, particularly seismic lines, are important conduits for wolves while hunting and traveling, especially during the snow-free months. Interestingly, this coincides with the time of the year when wolf-caused caribou mortality is highest (McLoughlin et al. 2003). However, it is unclear whether alternative predators such as coyotes and black bears use anthropogenic linear features to access and move around caribou range, particularly during the calving season when the effect of these predators is hypothesized to be most important from the perspective of caribou conservation.

In this study, we examined seasonal coyote and black bear use of industrial linear features and rivers and streams (i.e. natural linear features). We used two methods to assess movement behavior relative to linear developments. First, we used step selection functions (SSF; Fortin et al. 2005) to assess fine-scale movement in relation to industrial linear developments, i.e. pipeline right-of-ways, all-season roads, and conventional seismic lines. We predicted that if industrial linear features are important conduits to animal movement, coyotes and black bears would be more likely to move closer to these features than expected at random. Second, we used coyote and black bear Global Positioning System (GPS) locations to create observed animal movement paths and assessed whether these followed industrial linear features more closely than a null model of simulated animal paths. We predicted that if these features were being used as movement corridors, observed paths would show less deviation from industrial linear features than simulated paths.

3 Objective

- Assess whether anthropogenic linear features influence coyote and black bear movements in woodland caribou range in northeastern Alberta, Canada.

4 Methods

4.1 Study area

We assessed the influence of industrial and natural linear features on movement behavior by coyotes and black bears in the West Side of the Athabasca River (WSAR) caribou range (Fig. 1) and in the Cold Lake Air Weapons (CLAWR) caribou range (Fig. 2), respectively. Both caribou ranges are located to the south of the Athabasca oil-sands deposits within the boreal plains ecozone in northeastern Alberta, Canada.

Industrial activity associated with the location and extraction of oil and gas reserves in northeastern Alberta dates back to the late 1960s. However, these activities increased almost 3-fold in the mid- to late-1990s (Schneider 2002; Tracz et al. 2010). We calculated that approximately 3% of WSAR and 2% of CLAWR had been disturbed by the energy sector by 2007. This estimate included an assumed 5-m width for conventional seismic lines, 30-m for pipelines, 30-m for roads, 1 ha for oil and gas wells, as well as the surface area associated with other energy sector facilities such as compressor stations, camps, and gravel pits.

Forest harvesting also increased throughout this period (Schneider 2002); however, because of the scarcity of merchantable timber in the caribou ranges (i.e. peatlands), logging was confined to upland forests adjacent to the caribou ranges. Energy sector and forestry activities have resulted in an average of 1.8 km/km² of combined linear developments per township in this area of the province (Schneider 2002). Conventional seismic exploration lines are the most pervasive linear development (Schneider 2002), whereas all-season and seasonal roads and trails, pipeline-right-of-ways, transmission lines, and low impact seismic lines occur at lower densities. Most of our study area in CLAWR fell within military jurisdiction and thus access to civilians was restricted; however, oil and gas extraction was prominent within this area year-round (Czetwertynski 2007).

Vegetation in both study areas consisted of a naturally fragmented mosaic of peatlands and upland mixed-woods, interspersed by numerous burn areas, marshes and swamps. Peatlands consisted of black spruce bogs and black spruce – tamarack fens. Labrador tea (*Ledum groenlandicum*), bog birch (*Betula pumila*), willows (*Salix* spp.), sedges (*Carex* spp.), peat moss (*Sphagnum* spp.), and a variety of terrestrial lichens dominated the ground cover in peatlands. During the snow-free season, peatlands were typified by shallow surface water: the water level in bogs was typically 40–60 cm below the surface, whereas in fens it was at or near the surface (Vitt 1994). Upland mixed-woods consisted primarily of trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and jack pine (*Pinus banksiana*). Topographic relief is minimal within WSAR and CLAWR (elevation varied from 500 to 800 m). Both study areas were

bisected by major rivers (the Athabasca River in WSAR and the Sand River in CLAWR) and were covered extensively by numerous smaller rivers and streams.

4.2 Telemetry data

Between January 2006 and March 2007, we caught nine coyotes in WSAR using modified foot-hold traps in summer and helicopter net-gunning in winter (University of Alberta Animal Care Protocol No. 471503). We fitted captured animals with a VHF ($n = 2$) or a GPS (GPS 3300, $n = 6$; GPS 4400S, $n = 1$) radiocollar (Lotek Wireless, Aurora, Ontario, Canada). We programmed coyote GPS radiocollars with a 30-min relocation schedule from late-April to mid-June in 2006 and with a 4-h relocation schedule for the remainder of the study (2006 to early-2008). We monitored radiocollars fortnightly by fixed-wing aircraft. Previous trials in Alberta using Lotek GPS collars (with a high number of channels) have demonstrated minimal GPS bias, suggesting that corrections were unnecessary (Hebblewhite et al. 2007).

Three of the nine radiocollared coyotes moved out of the study area shortly after being collared. We assumed that these long-distance movements represented dispersal. None of these dispersers established a home range so we defined them as transients. Only five of the remaining six coyotes carrying functional radiocollars provided enough GPS locations to include in statistical analyses. If individuals were monitored for more than 1 year, data from separate years were combined.

Sixteen black bears were captured in CLAWR between 2001 and 2003, using L-83 ground snares (Lemieux & Czetwertynski 2006). Once restrained, bears were immobilized with tiletamine–zolazepam (University of Alberta Animal Care Protocol No. 322104) and equipped with GPS 2200L radiocollars (Lotek Wireless Inc., Newmarket, Ontario, Canada). Access permits within the CLAWR allowed trapping of bears within 1 km of roads; access was further restricted by peatlands scattered throughout the study area (Czetwertynski 2007). GPS radiocollars were programmed to record hourly fixes. If individuals were monitored for more than 1 year, data from separate years were combined.

To assess black bear movements relative to natural and industrial linear features we defined two seasons: caribou calving (from den emergence around mid-Apr. to 30 Jun.) and out of caribou calving (1 Jul. to hibernation around mid-Oct.). For coyotes, we defined two seasons: snow (Oct. to Mar.) and snow-free (Apr. to Sep.), and also analyzed movement patterns during the caribou calving season (15 Apr. to 30 Jun.), which overlapped partially with the snow-free season.

We were only interested in bio-physical factors that influenced black bear and coyote movement; so we excluded GPS locations associated with known den sites from the analyses. We did this by removing any locations within a 50-m-radius circular buffer around each black bear den between 11 Apr. (earliest available date) and 15 May (Latham et al. 2011b). We did not know the location of coyote dens so we assumed that den-associated locations would be discarded as inactive locations (see below).

4.3 Statistical analysis

4.3.1 Coyote and black bear step selection

Animal movement can be described as a series of steps (i.e. the straight line connecting two consecutive telemetry locations) and turns (i.e. the change in direction between two consecutive steps; Turchin 1998). We used SSF (Fortin et al. 2005; Coulon et al. 2008; Roever et al. 2010) to investigate whether the locations of coyote or black bear steps in the landscape were influenced by the proximity to industrial and natural linear features. This approach assumes that landscape characteristics along and/or at the end of the step can influence the probability of an animal taking that step, i.e. environmental characteristics between the start and end points of the step influence animal movements (Fortin et al. 2005). The relative probability of selecting a step is estimated by comparing observed animal steps with random steps using a case-control design (Fortin et al. 2005).

Coyote telemetry locations occurring < 4 h apart were subsampled so that only 4-h time steps were used in analysis. For black bears, telemetry locations were subsampled at 2-h intervals (i.e. a similar time interval was used for wolves by Latham et al. (2011c)) to reduce the potential for spatial autocorrelation resulting from using successive locations separated by only 1 h. We estimated SSF using steps taken by coyotes or black bears while traveling, which we defined to be the period during which each animal was actively moving from one point to another. Traveling steps were identified as all steps that occurred between bouts of inactivity; periods of inactivity were identified as ≥ 3 consecutive steps < 100 m, because such short-distance moves are often associated with resting-sites or kill-sites and result in no net displacement (Jerde & Visscher 2005). Steps during bouts of inactivity were discarded from analyses.

Observed steps were each compared to 25 random steps, each pair sharing the same starting point but differing in their lengths and turning angles (Fortin et al. 2005). Lengths and turning angles of random steps were drawn from step length and turning angle distributions based on the observed movements of monitored coyotes and black bears. Separate step length and turning angle distributions were created for the snow, snow-free, and caribou calving seasons for coyotes. Likewise, separate step length and turning angle distributions were created for the caribou calving and non-caribou calving seasons for black bears. In addition, we created separate step length and turning angle distributions for males and female bears because previous research demonstrated sex-related behavioral differences (Carter et al. 2010). Kolmogorov–Smirnov tests (Zar 1996) were used to assess differences between seasonal distributions; we combined those pairs that were not significantly different. For coyotes, step length distributions were not significantly different between snow and snow-free seasons ($D = 0.039$, $P = 0.201$) and thus were combined into one distribution based on 3055 steps. However, step length distributions were significantly different in and out of the caribou calving season ($D = 0.070$, $P = 0.008$), thus we created a distribution based on 731 step lengths for the coyote SSF analysis during the caribou calving season. Coyote turning angle distributions were not significantly different either between snow and snow-free seasons ($D = 0.032$, $P = 0.519$) or in versus outside of the caribou calving season ($D = 0.053$, $P = 0.139$) and thus were combined into one distribution based on 2589 turning angles. For black bears, the distribution of step lengths was significantly different between males and females and in and out of the caribou calving season (all $P < 0.05$), thus we created four separate step

length distributions. Turning angle distributions were not significantly different between males and females outside of the caribou calving season ($D = 0.036$, $P = 0.157$), so they were combined into one distribution. Turning angle distributions were significantly different between males and females during the caribou calving season ($D = 0.042$, $P = 0.042$), thus we created two separate distributions.

We estimated SSF using conditional logistic regression, which can expose the influence of environmental heterogeneity on animal movements by revealing where animals are most likely to be found at the end of each step (Fortin et al. 2005). We characterized observed and random steps based on the distance to linear features along the step (average, minimum, and maximum distance to covariate) and at the end of the step. We selected the most parsimonious method of collecting explanatory variables for each step through a model selection approach based on the Bayesian Information Criterion (BIC). Landscape covariates included all-season road (including paved and maintained gravel roads open to year-round vehicle use), pipeline right-of-way, conventional seismic line, major river, and minor river/stream. We obtained covariate data from industrial linear feature layers and the Alberta base features single line network (rivers and streams). We converted line shapefiles into distance to (km) raster layers (25×25 m pixels) using ArcGIS 10 (ESRI 2011).

We also used model selection (based on BIC) to estimate the influence of linear features on animal movements, rather than assuming an effect of distance based on a hypothetical range of perception of the animal. We did this by comparing alternative plausible models that included unconstrained distance variables (see Leblond et al. 2011) with models where distance variables were truncated to maximum effect distances of 0.5, 1, 1.5, 2, 2.5, and 3 km. For each explanatory variable, we selected the most supported (i.e. lowest BIC) distance-effect form.

Once we had determined the best-supported method to collect explanatory variables, and the best-supported distance-effect for each linear feature, we assessed multi-collinearity between the selected predictor variables using Pearson pair-wise correlation coefficients (Zar 1996). All variables had pair-wise correlation coefficients $|r_p| < 0.6$, thus we fitted a global model that included all of the covariates of interest, and inferred their positive, negative or lack of influence on fine-scale seasonal movements. We used this approach rather than comparing multiple alternative models because we were interested in assessing the effect of each linear feature type on animal movement. We also included step length as a covariate in the global model because Forester et al. (2009) showed this reduces bias in parameter estimates arising from using an empirical sampling method to obtain random points under strong levels of selection.

4.3.2 Simulated versus observed movement paths

We tested whether coyotes and black bears followed industrial and natural linear features as movement corridors by comparing the average deviation from these features of the observed traveling paths against a null model of simulated paths. We defined traveling paths as a series of consecutive traveling steps (see definition above), starting immediately after a bout of inactivity and finishing at the next inactive location. For coyotes, we used the 4-h traveling steps identified in the SSF analysis to define traveling paths; however, for black bears we used traveling steps identified from 1-h GPS locations

(as opposed to 2 h in SSF analyses) to obtain a more accurate description of each black bear traveling path. This analysis was performed seasonally for both species using the seasonal definitions described in the Telemetry Data section.

For a valid comparison between observed and simulated paths, the shape of the simulated paths should be similar to the observed paths except for their responses to linear features. Accordingly, we created simulated paths based on a Correlated Random Walk (CRW) model (Turchin 1998) using parameters derived from the observed telemetry data. Simulated paths were created by randomly drawing individual step lengths and turning angles from observed coyote and black bear step length and turning angle distributions. For coyotes, we used the same step length and turning angle distributions as for the SSF analysis. For black bears, we had to create new step length and turning angle distributions based on 1-h traveling steps. The distribution of 1-h step lengths was significantly different between males and females and during versus outside of the caribou calving season (all $P < 0.05$), resulting in four separate step-length distributions. Turning angle distributions were not significantly different between males in and out of the caribou calving season ($D = 0.022$, $P = 0.309$), so they were combined into one distribution. Turning angle distributions were significantly different between females in and out of the caribou calving season ($D = 0.035$, $P = 0.008$), thus we created two separate turning-angle distributions.

We discarded observed coyote or black bear paths consisting of only one step because we considered that was insufficient to assess whether the animals were truly following the linear features. We simulated the same number of paths as the number of paths observed for each species during each season, and also constrained the whole length of the simulated paths to occur within the study area. For coyotes, we set the number of steps within each simulated path at seven for the snow season and six for the snow-free and caribou calving seasons, i.e. the seasonal average number of steps per observed coyote path. For black bears, we set the number of steps within each simulated path at five for both of the seasons analyzed. The simulation of a relatively small number of steps per path is supported by the fact that CRW models often fail to predict empirical patterns over long periods, but represent reasonable null models for short series of movements (Turchin 1998).

Once we had defined and created observed and simulated coyote and black bear movement paths, we collected linear features covariates for each path as the length-weighted mean (LWM) (Beyer 2009) distance to pipeline right-of-ways, all-season roads, conventional seismic lines, and minor rivers/streams. For each type of linear feature, we calculated LWM by dividing a path into multiple 25-m segments (i.e. the resolution of our raster layers), multiplying the length of each segment by the distance of that segment to the nearest linear feature, adding these values across all segments of a path, and finally dividing that sum by the total length of the path. We considered LWM to represent the average deviation of a given path from perfect (i.e. no deviation shown by the animal following the linear feature, in which case LWM would be 0). We did not include major rivers in this analysis given their rarity in both study areas.

To assess whether there were significant differences between observed and simulated paths, we compared the distribution of observed and simulated deviations (LWM) from each type of linear feature using a two-sample Kolmogorov–Smirnov test (Zar 1996).

All statistical analyses were performed using the R software version 2.10.1 (R Development Core Team 2009).

5 Results

5.1 Step selection analysis

5.1.1 Coyotes

We obtained 8431 locations from GPS radiocollars deployed on five coyotes between January 2006 and March 2008. After rarifying the data to a 4-h fix rate, we were left with 4368 telemetry locations from which we identified 1391 and 1661 traveling steps taken during the snow and snow-free seasons, respectively. The average number of traveling steps per coyote was 278 (range: 98–644, $n = 5$) and 554 (range: 543–572, $n = 3$) during the snow and snow-free seasons, respectively. During the caribou calving season, we identified 729 traveling steps taken by three coyotes, with an average of 243 steps per animal (range: 176–307).

We observed strong support for models including explanatory variables collected at the end of each coyote step over models including variables collected along the step (Table 1). This was consistent across all seasons analyzed. Further, we observed strong support for spatially constrained rather than unconstrained distance effects for most linear feature types analyzed (Table 2).

Our results showed that coyote movements were influenced by several types of linear features (Table 3). During the snow season, traveling coyotes were more likely to select steps that took them further from a pipeline if the pipeline was ≤ 1.5 km away; if the pipeline was further than 1.5 km then the influence on coyote step selection was not as strong. The opposite pattern was observed during the snow-free and caribou calving seasons, when coyotes were more likely to select steps that took them closer to a pipeline if the pipeline was ≤ 0.5 km away. The average distance of traveling steps to the nearest pipeline was 1.62 ± 0.05 km (mean \pm SE) and 0.82 ± 0.02 km in the snow and snow-free seasons, respectively. The average distance of random steps to the nearest pipeline was 1.62 ± 0.05 km and $0.90 \text{ km} \pm 0.03$ km during the snow and snow-free seasons, respectively.

All-season roads influenced coyote travel during the snow and snow-free seasons, but not during the caribou calving season (Table 3). The relationship between step selection and distance to road was negative, indicating that coyotes were more likely to select steps that took them closer to all-season roads. However, there was a variable distance effect of roads, i.e. during the snow season coyote travel was influenced by roads that were within 1 km whereas during the snow-free season coyote travel was influenced by roads within half that distance (Table 3). During the snow season, the average distance of coyote traveling steps to the nearest road was 2.17 ± 0.11 km, while in the snow-free season it was 1.65 ± 0.04 km. The average distance of random steps to the nearest all-season road was 2.26 ± 0.11 km and 1.71 ± 0.04 km during the snow and snow-free seasons, respectively.

Conventional seismic lines had significant effects on coyote movements, though this varied with season. During the snow and caribou calving seasons, traveling coyotes showed selection of steps that brought them closer to a conventional seismic line. However, during the snow-free season coyotes showed neither selection nor avoidance of conventional seismic lines (Table 3).

Regardless of season, coyotes were more likely to take steps that would take them closer to a minor river or stream if these were relatively close (i.e. within 1 km). Distance to major rivers had significant effects on coyote movement in all seasons, when traveling wolves were more likely to take a step that would take them closer to a major river if the river was ≤ 2.5 km away. If the major river was > 2.5 km away, their influence on coyote movement during the snow-free and calving seasons was not strong.

5.1.2 Black bears

We obtained 40 439 locations from GPS radiocollars deployed on 16 black bears between May 2001 and October 2003. After rarifying the data to a 2-h fix rate and discarding 471 locations associated with dens, we were left with 20 216 telemetry locations from which we identified 5589 and 5600 traveling steps taken in and out of the caribou calving season, respectively. The average number of traveling steps per black bear was 373 (range: 196–747, $n = 15$) and 350 (range: 30–761, $n = 16$) in and out of the caribou calving season, respectively.

We observed strong support for models including explanatory variables collected at the end of each black bear step over models including variables collected along the step (Table 4). This was consistent across both seasons analyzed. Further, we observed strong support for spatially constrained rather than unconstrained distance effects for most linear feature types analyzed (Table 5).

Our results showed that black bear movements were influenced by all types of industrial linear features (Table 6). During both of the seasons analyzed, traveling black bears were more likely to select steps that took them closer to a pipeline and to an all-season road if the pipeline or road was ≤ 0.5 km away; if the pipeline or road was further than 0.5 km then the influence on black bear step selection was not as strong. The average distance of black bear traveling steps to the nearest pipeline was 0.56 ± 0.01 km and 0.60 ± 0.01 km during versus outside of the calving season, respectively. The average distance of random steps to the nearest pipeline was 0.61 ± 0.01 km and 0.66 ± 0.01 km during versus outside of the calving season, respectively. During the caribou calving season, the average distance of black bear traveling steps to the nearest road was 2.76 ± 0.04 km, while outside of the caribou calving season it was 3.18 ± 0.05 km. The average distance of random steps to the nearest all-season road was 2.85 ± 0.04 km and 3.24 ± 0.05 km during versus outside of the calving season, respectively.

Conventional seismic lines had significant effects on black bear movements during both seasons analyzed, with traveling black bears showing selection for steps that brought them closer to a conventional seismic line. However, there was a variable distance effect of seismic lines, i.e. during the caribou calving season black bear travel was influenced by all seismic lines whereas outside of the calving season black bear travel was influenced more strongly by seismic lines that were within 0.5 km (Table 6).

The influence of natural linear features on black bear step selection was variable. Black bears were more likely to take steps that would take them closer to a minor river or stream if these were relatively close (i.e. within 0.5 km) during the caribou calving season; conversely, minor rivers/streams did not influence step selection outside of the caribou calving season. Distance to major rivers had contrasting significant effects, with traveling black bears selecting steps that would take them closer to a major river during the caribou calving season, whereas the opposite was observed outside of the caribou calving season.

5.2 Simulated versus observed movement paths

5.2.1 Coyotes

We identified 447 movement paths with more than two steps for the five coyotes analyzed, with 175 paths occurring in the snow season and 272 in the snow-free season. A subset of 106 paths occurred during the caribou calving season. The number of paths per coyote ranged from 23 to 139, whereas the average number of steps per movement path was 7.5 and 5.9 during the snow and snow-free seasons, respectively, with an annual average of 6.6 steps (range: 1–57). The average length of coyote paths was 6.68 km in the snow season and 5.36 km in the snow-free season. The longest coyote traveling path was 64.64 km (57 individual successive steps) and was recorded in the snow season, while the longest individual coyote step (i.e. 4-h straight-line movement) recorded was 9.60 km and occurred during the snow-free season.

The deviation of observed and simulated coyote traveling paths from pipelines and conventional seismic lines was not significantly different during the snow season (Table 7). Conversely, snow-season coyote paths showed less deviation from (i.e. followed more closely) minor rivers and streams than did simulated paths. Observed snow-season coyote paths showed greater deviation from all-season roads than simulated paths (Table 7).

Coyote paths showed less deviation from (i.e. followed more closely) pipelines and all-season roads during the snow-free season. They also deviated less from minor rivers and streams than did simulated paths. Conversely, the deviation of observed snow-free season coyote paths from conventional seismic lines was not significantly different from that of simulated paths.

The same pattern found in the snow-free season was observed for most linear feature types (except minor rivers and streams) during the caribou calving season. During caribou calving, the deviation of observed coyote traveling paths from natural linear features was not significantly different from that of simulated paths.

5.2.2 Black bears

The GPS radiocollars on 16 black bears yielded 40 439 1-h telemetry locations, from which we identified 3903 movement paths with more than two steps, with 1919 and 1984 paths occurring in and out of the caribou calving season, respectively. The number of paths per black bear ranged between 8 and 557, whilst the average number of steps per movement path was 5.1 in and out of the caribou calving season (range: 2–34). The

average length of black bear paths was 2.36 km and 2.14 km during versus outside of the calving season, respectively. The longest black bear traveling path was 21.19 km (15 individual successive steps) and was recorded outside of the caribou calving season. The longest individual black bear step (i.e. 1-h straight-line movement) recorded was 4.21 km and also occurred outside of the caribou calving season.

During the caribou calving season, black bear traveling paths showed less deviation from (i.e. followed more closely) pipelines, all-season roads, and conventional seismic lines (Table 8). Likewise, black bear paths showed less deviation from minor rivers and streams than did simulated paths. Outside of the calving season, the same pattern was observed for most linear feature types except for minor rivers and streams as black bear traveling paths were not significantly different from simulated paths (Table 8).

6 Discussion

We assessed coyote movements relative to industrial and natural linear features during the snow and snow-free seasons, as well as during the caribou calving season (15 Apr. to 30 Jun.). Irrespective of season, we found that coyotes moved toward natural linear features such as rivers and streams and that coyote movement paths deviated less from these features than random paths. Previous studies have reported that rivers and streams are important features for coyotes, probably because frozen rivers in snow-covered months and river banks in snow-free months provide easy travel, and because these are areas that have high prey abundance (Atwood & Gese 2010). We suggest that coyote selection for rivers and streams in WSAR was similarly related to both movement and hunting. During the snow-free months, coyotes consumed a high proportion of muskrat (*Ondatra zibethicus*), which are abundant along the slow-moving, tortuous rivers and streams and other riparian features in WSAR (Latham et al. in review). Increased use of rivers and streams in peatlands by wolves hunting beaver resulted in increased spatial overlap between wolf pack territories and caribou range during snow-free months (Latham et al. 2011a). A similar mechanism might occur with coyotes and caribou, but driven by resource partitioning between wolves and coyotes, i.e. wolves consumed a high proportion of beaver but little muskrat, whereas the opposite pattern was found for coyotes (Latham et al. in review). During the snow season, canids might select frozen rivers and streams primarily because they provide greater ease of travel as the snow tends to be scoured from these features more than from the surrounding forest.

Our results support the hypothesis that coyote traveling behavior in caribou range and adjacent uplands is affected by industrial linear features. However, coyote use of industrial linear features as movement corridors differed between the type of line and season. Coyotes moved towards pipelines and their observed traveling paths followed pipelines more closely than simulated paths during the snow-free months and the caribou calving season. Similarly, coyotes selected steps that took them closer to all-season roads and their traveling paths showed less deviation from roads than simulated paths during the snow-free season. There are a few possible explanations why coyotes might be attracted to pipelines and road verges. First, coyotes may be attracted because of a higher availability of rodents on these features, since pipelines and road verges are mown on a regular basis in WSAR, which encourages the growth of grasses, a main food source for small rodents. Mouse and vole (*Peromyscus* spp., *Myodes* spp., and *Microtus* spp.) composed more than one-third of the diet of coyotes in WSAR during snow-free months

(Latham et al. in review). Second, pipelines and roads may provide coyotes with a refuge from wolf harassment, as wolves often avoid these features (Latham et al. 2011c), particularly when human activity is high on or near them (Whittington et al. 2005; Hebblewhite & Merrill 2008). Last, coyotes may be attracted to these features because of novel food sources such as garbage disposed of by oil and gas workers, road-killed animals, and/or the remains of hunter-killed animals. However, this is less likely as coyotes should similarly show strong selection for roads and pipelines during the snow season if the availability of novel food sources was the sole driver. We did not find this; rather influences of these features on coyote movements during the snow season were more variable, and not as strong as during the snow-free season.

Traveling coyotes selected steps that took them closer to conventional seismic lines during the snow season but not during the snow-free season. Given that Latham et al. (2011c) found that wolves selected seismic lines to move around caribou range in snow-free months, coyotes may be avoiding seismic lines during these months in an attempt to avoid interactions with wolves. Coyotes also selected steps closer to seismic lines during the calving season, suggesting that, like wolves, these features are important conduits for traveling (at least seasonally) in caribou range. Even though our SSF analysis showed selection for seismic lines at some times of the year, our analysis of observed versus simulated movement paths showed that coyote paths did not follow these features more closely than simulated paths in all the seasons that we analyzed. Thus, coyotes select seismic lines in the snow season, but tend not to use them as travel corridors over long distances, possibly because most are covered in deep snow. We speculate that because wolves do not select these features in winter (Latham et al. 2011c), coyotes minimize the risk of encounters with wolves near these features or coyotes gain benefits associated with high prey abundance close to these features. Similar adaptive changes in coyote resource selection based on the perception of the level of wolf activity have been reported by Atwood and Gese (2010) in the Greater Yellowstone Ecosystem, whereby coyotes shared the same space as wolves but adapted their fine-scale behaviors to minimize the risk of encounters and thus the potential for aggressive interactions.

Industrial linear features influenced black bear movements more consistently than did coyote movements. We found that black bears selected steps that took them closer to pipelines, all-season roads, and conventional seismic lines in all seasons. Likewise, observed black bear movement paths showed less deviation from all industrial linear feature types than simulated paths during all seasons. Previous research suggested that the importance of roadsides for black bears is related to the abundance of high-quality forage (Bastille-Rousseau et al. 2011). We suggest that bears may also find high-quality forage on pipelines and seismic lines, because these features have been commonly revegetated with clover (*Trifolium* spp.) in Alberta, which is a preferred food for bears during spring and early summer (Boileau et al. 1994). Czetwertynski (2007) suggested that high use of industrial linear features in CLAWR might also be related to the prohibition of hunting in this area, which would allow bears to forage these resources unmolested relative to areas where hunting is permitted. However, Roever et al. (2010) showed that grizzly bears in the foothills of Alberta (a non-hunted species in Alberta) selected steps closer to roads irrespective of the level of human use. The primary mortality risk associated with roads for grizzly bears is poaching and the potential for collisions with vehicles, but despite these risks, they still selected steps closer to roads. Thus, irrespective of bear species or risk to those species, strong selection for industrial linear features suggests that the

nutritional benefits associated with industrial linear features outweigh the risks associated with these features, potentially resulting in an attractive sink (Delibes et al. 2001).

In eastern Canada, Bastille-Rousseau et al. (2011) showed that black bears did not select areas with a high probability of encounter with ungulate neonates. This suggests that although black bears select and use industrial linear features as movement corridors in caribou range, this behavior might not be related to actively hunting caribou calves and thus does not necessarily result in increased risks for caribou. However, Bastille-Rousseau et al. (2011) also showed that black bears moved frequently and preferentially between vegetation-rich areas (e.g. roadsides), and suggested that this behavior could result in high rates of fortuitous encounters with neonates even if bears were not actively searching for them. Thus, black bear use of industrial linear features offering abundant forage could still negatively impact caribou populations, even though caribou tend to avoid these features (Dyer et al. 2001). This could occur through increased incidental encounters and predation if these features occur close to patches of peatland habitat suitable for caribou.

Our study provides the first detailed assessment of fine-scale seasonal coyote and black bear use of industrial linear features in woodland caribou range. We found that coyote selection for industrial linear features as movement corridors was variable, whereas selection for natural linear features such as rivers and streams was more consistent year-round. Conversely, black bears showed strong selection and used industrial linear features as movement corridors during both of the seasons analyzed. Selection and use of industrial linear features by these predators, in addition to wolves (as shown by Latham et al. 2011c), could negatively impact prey such as caribou via increased incidental predation. Using simulation modeling, McKenzie et al. (2012) showed that encounter rates between wolves and their prey were significantly higher in landscapes with high densities of industrial linear features and were most pronounced at low prey densities (as is the case with woodland caribou). A similar phenomenon could result from coyotes and black bears using these features. McKenzie et al. (2012) also predicted that prey would experience high risk of mortality in environments with a high linear-feature density unless they learned to avoid these features. In fact, Dyer et al. (2001) showed that caribou do avoid roads and seismic lines. However, as the density of linear features increases in the landscape, the ability of caribou to avoid these features by biologically-meaningful distances will decrease as will their ability to spatially separate from predators, resulting in functional loss of otherwise suitable habitat and increased incidental predation.

7 Acknowledgements

Funding and support was provided by the Alberta Bowhunters Association, Alberta Caribou Committee, Alberta Conservation Association, Alberta Cooperative Conservation Research Unit, Alberta Fish and Game Association, Alberta-Pacific Forest Industries, Alberta Professional Outfitters Society, Alberta Sustainable Resource Development, Canadian Wildlife Federation, NSERC Integrated Landscape Management Chair, Pope and Young Club, Sustainable Forest Management Network, Safari Club International, and the University of Alberta. Special thanks are given to the Canadian Association of Petroleum Producers and Petroleum Technology Alliance Canada for the funding provided via the 2006 and 2007 Environmental Research Advisory Council Broad Industry Initiatives Caribou Funding, and the 2010 and 2011 Alberta Upstream

Petroleum Research Fund. ADML was supported by an Izaak Walton Killam Memorial Scholarship. We are grateful to numerous field assistants and pilots. We thank S. Czetwertynski, R. Lemieux, and F. Schmiegelow for assistance with black bear data, and personnel at the Department of National Defence (4-Wing, Cold Lake, Alberta) for access to the Cold Lake Air Weapons.

8 References

- ASRD [Alberta Sustainable Resource Development], ACA [Alberta Conservation Association] 2010. Status of the woodland caribou (*Rangifer tarandus caribou*) in Alberta: Update 2010. Edmonton, Alberta, Canada, Alberta Sustainable Resource Development Wildlife Status Report 30.
- Atwood TC, Gese EM 2010. Importance of resource selection and social behavior to partitioning of hostile space by sympatric canids. *Journal of Mammalogy* 91: 490–499.
- Ballard WB 1994. Effects of black bear predation on caribou: a review. *Alces* 30: 25–35.
- Bastille-Rousseau G, Fortin D, Dussault C, Courtois R, Ouellet J-P 2010. Foraging strategies by omnivores: are black bears actively searching for ungulate neonates or are they simply opportunistic predators? *Ecography* 34: 588–596.
- Bergerud AT 1974. Decline of caribou in North America following settlement. *Journal of Wildlife Management* 38: 757–770.
- Bergerud AT, Butler HE, Miller DR 1984. Antipredator tactics of calving caribou: dispersion in mountains. *Canadian Journal of Zoology* 62: 1566–1575.
- Beyer HL 2009. Geospatial modelling environment. Available at <http://www.spatalecology.com/gme/>
- Boertje RD, Valkenburg P, Mcnay ME 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. *Journal of Wildlife Management* 60: 474–489.
- Boileau F, Crête M, Huot J 1994. Food habits of the black bear, *Ursus americanus*, in Gaspésie Park, eastern Quebec. *Canadian Field-Naturalist* 108: 162–169.
- Bowen WD 1981. Variation in coyote social organization: the influence of prey size. *Canadian Journal of Zoology* 59: 639–652.
- Carter NH, Brown DG, Etter DR, Visser LG 2010. American black bear habitat selection in northern Lower Peninsula, Michigan, USA, using discrete-choice modeling. *Ursus* 21: 57–71.
- COSEWIC [Committee on the Status of Endangered Wildlife in Canada] 2002. COSEWIC assessment and update status report on the woodland caribou, *Rangifer tarandus caribou*. Ottawa, Ontario, Canada, Environment Canada.

- Coulon A, Morellet N, Goulard M, Cargnelutti B, Angibault J-M, Hewison AJM 2008. Inferring the effects of landscape structure on roe deer (*Capreolus capreolus*) movements using a step selection function. *Landscape Ecology* 23: 603–614.
- Crête M, Desrosiers A 1995. Range expansion of coyotes, *Canis latrans*, threatens a remnant herd of caribou, *Rangifer tarandus*, in southeastern Québec. *Canadian Field-Naturalist* 109: 227–235.
- Cumming HG 1992. Woodland caribou: facts for forest managers. *Forestry Chronicle* 68: 481–491.
- Czetwertynski SM 2007. Effects of hunting on the demographics, movement, and habitat selection of American black bears (*Ursus americanus*). Unpublished PhD thesis, Department of Renewable Resources, University of Alberta, Edmonton, Canada.
- Delibes M, Gaona P, Ferreras P 2001. Effects of an attractive sink leading into maladaptive habitat selection. *American Naturalist* 158: 277–285.
- Dyer SJ, O’Neill JP, Wasel SM, Boutin S 2001. Avoidance of industrial development by woodland caribou. *Journal of Wildlife Management* 65: 531–542.
- Environment Canada 2008. Scientific review for the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada. Ottawa, Ontario, Canada, Environment Canada.
- ESRI [Environmental Systems Research Institute] 2011. ArcGIS Desktop: release 10. Redlands, CA, USA, Environmental Systems Research Institute.
- Forester JD, Kyung Im H, Rathouz PJ 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology* 90: 3554–3565.
- Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86: 1320–1330.
- Fournier N, Faubert R 2001. Évaluation du troupeau de caribous de la Gaspésie. Direction de l’aménagement de la faune Gaspésie – Îles-de-la-Madeleine. Sainte-Anne-des-Monts, Québec, Canada, Canada Société de la Faune et des Parcs du Québec. [In French.]
- Franzmann AW, Schwartz CC, Peterson RO 1980. Moose calf mortality in summer on the Kenai Peninsula, Alaska. *Journal of Wildlife Management* 44: 764–768.
- Fuller TK, Keith LB 1981. Non-overlapping ranges of coyotes and wolves in northeastern Alberta. *Journal of Mammalogy* 62: 403–405.
- Hayes RD, Farnell R, Ward RMP, Carey J, Dehn M, Kuzyk GW, Baer AM, Gardner CL, O’Donoghue M 2003. Experimental reduction of wolves in the Yukon: ungulate responses and management implications. *Wildlife Monographs* 152: 1–35.

- Hebblewhite M, Merrill E 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology* 45: 834–844.
- Hebblewhite M, Percy M, Merrill EH 2007. Are all GPS collars created equal? A comparison of three brands for habitat-induced fix-rate bias. *Journal of Wildlife Management* 71: 2026–2033.
- Hummel M, Ray J C 2008. *Caribou and the North: a shared future*. Toronto, Ontario, Canada, Dundurn Press.
- James ARC 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta. Unpublished PhD thesis, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.
- James ARC, Stuart-Smith AK 2000. Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management* 64: 154–159.
- James ARC, Boutin S, Hebert DM, Rippin AB 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *Journal of Wildlife Management* 68: 799–809.
- Jerde C, Visscher D 2005. GPS measurement error influences on movement model parameterization. *Ecological Applications* 15: 806–810.
- Kunkel KE, Mech LD 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. *Canadian Journal of Zoology* 72: 1557–1565.
- Latham ADM 2009. Wolf ecology and caribou-primary prey-wolf spatial relationships in low productivity peatland complexes in northeastern Alberta. Unpublished PhD thesis, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.
- Latham ADM, Latham MC 2011. Coyotes invade woodland caribou range. *Kararehe Kino/Vertebrate Pest Research* 19: 6–7.
- Latham ADM, Latham MC, McCutchen NA, Boutin S 2011a. Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *Journal of Wildlife Management* 75: 204–212.
- Latham ADM, Latham MC, Boyce MS 2011b. Habitat selection and spatial relationships of black bears (*Ursus americanus*) with woodland caribou (*Rangifer tarandus caribou*) in northeastern Alberta. *Canadian Journal of Zoology* 89: 267–277.
- Latham ADM, Latham MC, Boyce MS, Boutin S 2011c. Movement responses by wolves to industrial linear features and its effect on woodland caribou in northeastern Alberta. *Ecological Applications* 21: 2854–2865.
- Latham ADM, Latham MC, Boyce MS, Boutin S In review. Spatial relationships of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) with woodland caribou

(*Rangifer tarandus caribou*) during the calving season in a human modified boreal landscape. *Wildlife Research*.

- Leblond M, Frair J, Fortin D, Dussault C, Ouellet J-P, Courtois R 2011. Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. *Landscape Ecology* 26: 1433–1446.
- Lemieux R, Czetwertynski S 2006. Tube and rubber padded snares for capturing American black bears. *Ursus* 17: 81–91.
- Mahoney SP, Abbott H, Russell LH, Porter BR 1990. Woodland caribou calf mortality in insular Newfoundland. In: Myrberget S ed. *Transactions of the 19th Congress of the International Union of Game Biologists* (Norwegian Institute for Nature Research, Trondheim, Norway). Pp. 592–599.
- McKenzie HW, Merrill EH, Spiteri RJ, Lewis MA 2012. How linear features alter predator movement and the functional response. *Interface Focus* 2: 205–216.
- McLoughlin PD, Dzus E, Wynes B, Boutin S 2003. Declines in populations of woodland caribou. *Journal of Wildlife Management* 67: 755–761.
- Nolan, JW, Barrett MW 1985. A preliminary study of moose calf mortality in northeastern Alberta. Vegreville, Alberta, Canada, Alberta Environmental Centre.
- Pinard V, Dussault C, Ouellet J-P, Fortin D, Courtois R 2012. Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. *Journal of Wildlife Management* 76: 189–199.
- R Development Core Team 2009. *R: A language and environment for statistical computing*. Vienna, Austria, R Foundation for Statistical Computing. ISBN 3-900051-07-0. (<http://www.R-project.org>)
- Roever LC, Boyce MS, Stenhouse GB 2010. Grizzly bear movements relative to roads: application of step selection functions. *Ecography* 33: 1113–1122.
- Schlegel M. 1976. Factors affecting calf elk survival in north central Idaho - a progress report. In: *Proceedings of the 56th Annual Conference of the Western Association of State Game and Fish Commissioners* (Western Association of State Game and Fish Commissioners: Sun Valley, Idaho). Pp. 342–355.
- Schneider RR 2002. *Alternative futures: Alberta's boreal forest at the crossroads*. Edmonton, Alberta, Canada, The Federation of Alberta Naturalists.
- Schneider RR, Hauer G, Adamowicz WL, Boutin S 2010. Triage for conserving populations of threatened species: the case of woodland caribou in Alberta. *Biological Conservation* 143: 1603–1611.
- Seip DR 1991. Predation and caribou populations. *Rangifer* 7 (Special Issue): 46–52.

- Tracz BV, LaMontagne JM, Bayne EM, Boutin S 2010. Annual and monthly range fidelity of female boreal woodland caribou in response to petroleum development. *Rangifer* 30: 31–44.
- Turchin P 1998. *Quantitative analysis of movement*. Sunderland, MA, USA, Sinauer Associates.
- Vitt DH 1994. An overview of factors that influence the development of Canadian peatlands. *Memoirs of the Entomological Society of Canada* 169: 7–20.
- Whittington J, St. Clair CC, Mercer G 2005. Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications* 15: 543–553.
- Wittmer HU, Sinclair ARE, McLellan BN 2005. The role of predation in the decline and extirpation of woodland caribou. *Oecologia (Berl.)* 144: 257–267.
- Zar JH 1996. *Biostatistical analysis*. 3rd edn. Upper Saddle River, NJ, USA, Prentice-Hall.