Landscape Composition and Configuration Influences Woodland Caribou Calf Recruitment

Sara C. McCarthy

A Thesis
in
The Department
of
Biology

Presented in Partial Fulfillment of the Requirements
for the Degree of Master of Science (Biology) at
Concordia University
Montreal, Quebec, Canada

August 2010

Your file Votre référence
ISBN: 978-0-494-71057-9
Our file Notre référence
ISBN: 978-0-494-71057-9

Contribution of Authors

As first author, I was responsible for the concepts, hypotheses, design, data gathering, GIS work, and data analysis. I also wrote the manuscripts and thesis.

Chapters 1 and 2 were co-authored by Dr. Robert B. Weladji, Christine Doucet, and Paul Saunders. Dr. Weladji served as a mentor, supervised the work, helped with many of the statistical analyses, and edited the manuscripts. Christine Doucet provided insight into the caribou conservation situation in Newfoundland, helped with important contacts, and provided feedback on an earlier draft of Chapter 1. Paul Saunders helped with a lot of the caribou collar location data upload and filtering as well as many of the other data provisions and technical issues, provided insight to the caribou conservation situation in Newfoundland, helped with important contacts, and provided feedback on an earlier draft of Chapter 1.

Dr. Weladji helped further with the correction of the thesis.

Abstract

Landscape Composition and Configuration Influences Woodland Caribou Calf Recruitment

Sara C. McCarthy

Newfoundland woodland caribou (*Rangifer tarandus caribou*) populations are in steep decline and disturbance-related habitat loss and fragmentation have been blamed for similar woodland caribou population declines across the country. Research has focused on caribou habitat selection, and there is a need for studies to focus on landscape components that can be managed, and their relationships with caribou vital rates. I quantified landscape composition and configuration within the calving/post-calving range (CPCR) of female woodland caribou belonging to six herds in Newfoundland to explore their influence on calf recruitment over four years. I identified the CPCR of radio-collared female caribou and calculated the total disturbance area (area of forest fires and area within 250m of human disturbance sources), area occupied by natural landcover types, and three fragmentation measures (effective mesh size, edge to area ratio, and fragmentation extent) for each female's CPCR, and averaging them yearly for each herd. Total disturbance area and the area occupied by mixed forests were found to have negative effects on calf recruitment, whereas no significant direct relationship was found between either of the fragmentation measures and calf recruitment. Using Information Theoretic Approach, I found that the most parsimonious model to explain variation in calf recruitment included total disturbance area, the area occupied by mixed forests and wetlands, and the edge to area ratio measure of fragmentation. The effect of total disturbance area was negative, while the effect of wetlands was positive. It appears that

combining quantitative measures of disturbance-related landscape structure (i.e. composition as well as configuration) to explain variation in woodland caribou calf recruitment, or other vital rates, would improve our ability to relate scientific research findings to wildlife management and land-use issues.

Contribution of Authors

As first author, I was responsible for the concepts, hypotheses, design, data gathering, GIS work, and data analysis. I also wrote the manuscripts and thesis.

Chapters 1 and 2 were co-authored by Dr. Robert B. Weladji, Christine Doucet, and Paul Saunders. Dr. Weladji served as a mentor, supervised the work, helped with many of the statistical analyses, and edited the manuscripts. Christine Doucet provided insight into the caribou conservation situation in Newfoundland, helped with important contacts, and provided feedback on an earlier draft of Chapter 1. Paul Saunders helped with a lot of the caribou collar location data upload and filtering as well as many of the other data provisions and technical issues, provided insight to the caribou conservation situation in Newfoundland, helped with important contacts, and provided feedback on an earlier draft of Chapter 1.

Dr. Weladji helped further with the correction of the thesis.

Acknowledgements

This thesis would not have been completed to such a standard, nor in such a time span without the dedicated endeavours of Dr. Weladji. His assurances, guidance, support, and expertise were crucial and I give many thanks for such a wonderful supervisor.

Conducting this study from Montreal would have been impossible without the wealth of information, contacts, and suggestions provided by Christine Doucet and Paul Saunders. Thank you to my committee members; Dr. Pascale Biron and Dr. James Grant, as well as to my lab members. There were many people who assisted with data provisions and technical issues, and I would like to acknowledge their help and influence in the timely completion of this project; A. Bernier, C. Breon, C. Soulliere, C. Dyke, M. Dyke, F. Earle, M. Flannigan, E. Girvetz, P. Grosman, A. Harris, J. Jaeger, D. Jennings, F. Kirby, B. Lawlor, J. Little, G. Luther, L. F. Madrinan, C. Marks, J. McGrath, J. Morrissey, L. Nolan, K. O'Driscoll, J. Strickland, J. Theau, and M. Wulder. Funding for this project was provided by National Sciences and Engineering Research Council of Canada (NSERC) Discovery grant to Dr. Weladji.

To my sidekick C-Jae, thanks for motivating me to get to the office every day, (or every other day!), in hopes of another afternoon of exploring life and its joys and challenges together. You were the best co-worker I could have asked for and I hope we find each other working together again someday. Amin, without you this would have been a time of stress and exhaustion, but you helped me find the balance between work and fun; your support and assurances mean so much to me. And finally, thank you to my family, who have given me the means to reach my goals, the desire and drive to do so, and the assurance that it's OK if I don't.

Table of contents

List of Figures

study caribou herds from 2005-2008. Outlined region in the inset represents the Grey River Management Zone, within which caribou hunting is prohibited.

Figure 6: Illustration of how each of our three fragmentation tools measure CPCR fragmentation. Area of the large circles (CPCRs), and total area of the components within the large circles (fragmentation factors), do not change from left to right. (A) represents decreasing effective mesh size, such that the changing configuration of the disturbance components decreases the probability of animals meeting without having to cross a disturbance zone, (A,B, and C) represent increasing edge to area ratio, such that the changing configuration of the disturbance components increases edge habitat without changing disturbed area, and (A, B, and C) represent increasing fragmentation extent, such that the changing configuration of the disturbance components decreases the potential for caribou to distance themselves away from disturbances, while remaining within the CPCR.

Figure 7: Difference between caribou herds in respect to average yearly (A) effective mesh size (a measure of area available before having to cross disturbance layer), (B) edge to area ratio (a measure of edge effects), and (C) fragmentation extent (a measure of whether disturbance layer is clumped or dispersed) from 2005-2008 in Newfoundland, Canada. Error bars are 1 SE of the mean. Abbreviations for herds: BU= Buchans, GA = Gaff Topsail, GR = Grey River, MP = Mount Peyton, LP = LaPoile, and PH = Pot Hill.

Figure 8: Observed calf recruitment (calves/100 females) from 2005-2008 in Newfoundland, Canada, versus calf recruitment (calves/100 females) as predicted by top AIC_c ranked linear mixed model (accounting for herd) with year as a random term; recruitment = herd + total disturbance + mixed forest + wetland + edge to area ratio. The

line represents where the points would lie if the model fit the observed calf recruitment perfectly.

List of Tables

General Introduction

Disturbance related habitat loss and fragmentation and the associated rise in predation risk have driven woodland caribou (*Rangifer tarandus caribou*) declines across their range (Rettie and Messier 2000, COSEWIC 2002, Apps and McLellan 2006). The footprint of human disturbances extends beyond structural limits when we consider caribou behavioural avoidance buffers (Dyer et al. 2001, Cameron et al. 2005, Courtois et al. 2007). These avoidance buffers further reduce functional habitat availability (Rettie and Messier 2000) and hence caribou body condition (Vistnes et al. 2001), reproductive success (Cameron et al. 2005), and population persistence (Wittmer et al. 2007, Sorensen et al. 2008). Some of these human disturbances, particularly forestry logging operations, are preferred by other ungulate species and their predators (Laliberte and Ripple 2004, Boisjoly et al. 2010) and therefore increase caribou predation rates (James and Stuart-Smith 2000, Wittmer et al. 2007). Conservation efforts often conflict with economic interests that favour industrial development and expansion. Consequently, a large majority of Canadian woodland caribou herds have been listed as threatened or at risk by COSEWIC (2002), yet the Newfoundland population still remains classified as not at risk.

Over the past decade, caribou census surveys across Newfoundland have uncovered an 85% drop in calf survival and an associated 66% decrease in population estimates (Mahoney et al. 2008). Predation by bears (*Ursus americanus*), coyotes (*Canis latrans*), lynx (*Lynx canadensis*), and bald eagles (*Haliaeetus leucocephalus*) has accounted for 90% of calf deaths (Mahoney et al. 2008). Forestry practices are a major threat to Newfoundland caribou and operate through clear-cut logging practices. There are few highways on the island, although forestry access roads branch in all directions and are often used for recreational purposes. There are also several mining sites, many small hydro electric generation sites, and a large oil/gas exploration project on the south-western shore. Small forest fires are common, although large burns have been minimal over the past 40 years. An old railroad stretches from east to west, but is now used only for recreational purposes (ATV trail). Agriculture is minimal and clustered close to residential areas. These landscape disturbances contribute to habitat loss and fragmentation, while promoting the growth of early forest stages, therefore creating spatial overlap between caribou territory, moose (*Alces americanus*) populations, and their associated predators (Laliberte and Ripple 2004, Boisjoly et al. 2010, Mosnier et al. 2008). Not only do existing predator populations increase or undergo range shifts with habitat disturbance, but their hunting efficiency and access to caribou also increases with the construction of linear features, such as power lines and roads (Jalkotzy et al. 1997, James and Stuart-Smith 2000).

Newfoundland caribou ecology research has focused on habitat selection and avoidance in relation to habitat disturbance. Mature coniferous forests have been identified as the most important habitat for woodland caribou persistence, as it provides prime foraging habitat and predator refuge (Bergerud 1972, Mahoney and Virgl 2003, Schaefer and Mahoney 2007). Open bogs and barrens have also been selected for predator avoidance, especially during the post-calving season, whereas early seral forest stages are avoided (Mahoney and Virgl 2003, Schaefer and Mahoney 2007). In general, human disturbances and forest fires were found to reduce caribou densities around the source, with avoidance zones ranging from 1 to 15 km (Chubbs et al. 1993, Mahoney and Schaefer 2002b, Mahoney and Virgl 2003, Schaefer and Mahoney 2007, Weir et al. 2007). Sensitivity to disturbance increased during the calving/post-calving season, especially for females with calves (Chubbs et al. 1993, Dyer et al. 2001).

Although informative, findings from these studies are difficult to relate to current conservation strategies. Decisions made by caribou regarding where to forage, calf, or spend a season can be affected by the level of disturbance in the area or the amount of quality habitat available (Gill et al. 2001). Failing to acknowledge these influences on habitat selection can lead to erroneous conclusions regarding habitat preference. Although these behavioural and spatial changes are assumed to translate into fitness costs, the magnitude and extent of these costs remain unknown. Hence from a conservation perspective, there is need for a shift from behavioural-type habitat selection/avoidance studies, towards studies that investigate elements that we can manage or influence, such as human disturbance, and their associations with important vital rates, such as population growth, survival, and reproduction (Gill and Sutherland 2000, Wittmer et al. 2007). Such studies have become feasible with increased use of user-friendly geographical information software such as ArcGIS (ESRI Inc., Redlands, California), as well as the availability of data from radio-collars, digital maps, and satellite images.

An exploration of possible relationships between landscape structure and vital rates is therefore warranted for Newfoundland woodland caribou, and would provide important information for conservation and land-use managers. This study examines how landscape composition (total disturbance and natural landcover type areas) and configuration (fragmentation via disturbance) influence caribou survival for six herds over four years.

As survival of calves during the first six months of life seems to be the limiting factor for Newfoundland populations (Mahoney et al. 2008), we chose to use calf recruitment measured as the number of calves per 100 adult females at the end of October as our measure of caribou survival. Landscape structure was evaluated at the May-October seasonal home range scale, which we termed the calving/post-calving range (CPCR).

This thesis has five objectives; the first three examine possible relationships between landscape composition and calf recruitment and are addressed in Chapter 1, and objectives four and five focus on the relationship between landscape configuration (fragmentation) and calf recruitment and are covered in Chapter 2. Objective #1 was to calculate the average total disturbance area inside CPCRs using digital maps of nine disturbance sources and assess whether there is a relationship between this total disturbance area and calf recruitment. Objective #2 was to calculate the average area occupied by eleven natural landcover types inside CPCRs using Landsat images, and determine whether the area of any of these landcover types were related to calf recruitment. Objective #3 was to identify the most parsimonious model to explain calf recruitment in terms of these measured composition parameters, using an information theoretic approach (Akaike 1973, Burnham and Anderson 2002).

For the second Chapter I used three novel approaches to measuring disturbance-mediated fragmentation that account for habitat loss; namely effective mesh size, edge to area ratio, and fragmentation extent. Objective #4 was to determine whether calf recruitment was related to either of these fragmentation measures. Objective #5 was to examine whether accounting for configuration could improve the previously-generated calf recruitment models (objective #3) by adding one of the fragmentation measures. By combining and quantifying the effects of total disturbance area, natural landcover types, and disturbance mediated fragmentation on calf recruitment, we may begin to see a clearer picture of how to generate comprehensive land-use plans, with caribou conservation taking precedence.

Chapter 1:

Landscape Disturbance Influencing Woodland Caribou Declines in Newfoundland

Sara, C. McCarthy[1], Robert B. Weladji[1], Christine Doucet[2], and Paul Saunders[2]

[1] Department of Biology, Concordia University, 7141 Sherbrooke Street W., Montreal, QC, H4B 1R6, Canada

[2] Wildlife Division, Newfoundland and Labrador Department of Environment and Conservation, 117 Riverside Drive, P. O. Box 2007, Corner Brook, NL, A2H 7S1, Canada

Abstract

Since the 1990's, Newfoundland's woodland caribou (*Rangifer taranadus caribou*) population has declined by an estimated 66%. Low calf recruitment has been blamed, possibly triggered by increasing calf predation or decreasing resources. To explore whether these pressures may be mediated by human-induced disturbance factors we studied the yearly (2005-2008) calving/post-calving range (CPCR) of 104 GPS collared females from six herds with estimated calf recruitment rates. We combined nine disturbance factors to create a total disturbance layer and mapped it onto LANDSAT images of natural landcover to quantify each herd's CPCR composition. We investigated how total disturbance area as well as landcover types influenced calf recruitment, and assessed the model that best explained variation in calf recruitment by combining these measures. We found calf recruitment to be negatively influenced by total disturbance and mixed forest area within CPCRs. Based on corrected Akaike Information Criterion, the best model combining disturbance and landcover types to explain variation in calf recruitment included total disturbance and deciduous forest area. This study highlights the possibility of using total disturbed area to model calf recruitment, as well as an association between human disturbance factors and caribou population declines. These quantitative methods, combined with future analysis of landscape fragmentation, may assist wildlife managers in determining effective conservation strategies.

Introduction

As human population growth and consumption increase, wilderness is often traded for industry, creating disturbance sources throughout landscapes (Leu et al. 2008). If these disturbances occur within the home range of sensitive wildlife populations, habitat loss and changing population dynamics may lead to population declines (Channell and Lomolino 2000). These disturbed areas may then support more generalist predators, who may add additional pressure to the sensitive secondary prey species through spill over exploitation (Crete and Desrosiers 1995).

Canada loses an average 50,000 hectares of forest per year due to land development, not including the additional areas temporarily disturbed by forest harvesting or fire (Natural Resources Canada 2009). For woodland caribou (*Rangifer tarandus caribou*) who require mature coniferous forests (Rettie and Messier 2000, Mahoney and Virgl 2003), the amount of habitat physically lost through human activities increases when we also consider functional loss via the disturbance behaviour of the caribou (Chubbs et al. 1993, Rettie and Messier 2000, Courtois et al. 2007, Vors et al. 2007).

Much research has concentrated on woodland caribou habitat selection (e.g. Chubbs et al. 1993, Rettie and Messier 2000, Gustine and Parker 2008, Hins et al 2009), but only a few have focused on direct relationships between habitat composition and vital rates (Nellemann et al. 2003, Wittmer et al. 2007, Sorensen et al. 2008). These studies have found that anthropogenic disturbance, fires, and associated early seral stage forests can be negatively related to both survival and reproduction. A shift in research objectives towards correlates of vital rates may be informative, considering avoidance of a particular landscape component does not imply elimination of any associated negative influence on vital rates.

Newfoundland caribou populations have declined by an estimated 66% since the 1990s and monitoring has suggested an associated decline in calf recruitment (calves/100 adult females) over the first six months of life (Mahoney et al. 2008). Industry has continued to spread across the island during this time; forestry, hydroelectric, mining, recreation, and transportation developments are all additive disturbance factors that have impacts differing across space and time. Combined with natural forest fires, these habitat alterations may hinder calf survival by fostering avoidance behaviours (Schaefer and Mahoney 2007, Weir et al. 2007), which can create higher densities (Nellemann and Cameron 1996), higher predation rates (James and Stuart-Smith 2000, Wittmer et al. 2005a), and reduced forage availability (Weladji and Forbes 2002, Mahoney and Virgl 2003, Gustine and Parker 2008).

Our goal was to assess the relationship between calf recruitment and landscape composition, focusing on the calving/post-calving range (CPCR) for woodland caribou herds in Newfoundland. We examined the area of total disturbance and landcover types within CPCRs, and assessed their relationship with calf recruitment of 6 herds over 4 years. We predicted that total disturbance area would be negatively related to calf recruitment. Among landcover types, preferred habitats such as coniferous forest, barrens, and wetlands were expected to display a positive trend with calf recruitment (Mahoney and Virgl 2003, Schaefer and Mahoney 2007, Hins et al. 2009). Conversely, commonly avoided habitats such as deciduous and mixed forests were predicted to have a negative association with calf recruitment (Mahoney and Virgl 2003, Wittmer et al. 2007, Hins et al. 2009). Finally, we searched for the best model that explained woodland caribou vital rates in relation to both total disturbance area and landcover parameters.

Material and Methods

Study Area

The study was conducted in the CPCR of six caribou herds across Newfoundland's interior (Fig 1). The majority of the rugged landscape has been shaped by ice scour and glacial deposits, creating lowlands with many streams, lakes, and ponds and elevations reaching 815 m. The area is extensively covered in forests of black spruce (*Picea mariana*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea)* with dense moss (*Hylocomium spp.*) carpets (Daaman 1983). There were also many shrublands, wetlands, and barrens. The climate is characterised by cool summers and winters with annual precipitation varying between regions (<1000 mm).

Newfoundland's woodland caribou are of the sedentary ecotype, and hence undergo smaller seasonal migrations than barren ground caribou (Bergerud 1996). During the calving/post-calving season, mature coniferous forests are highly preferred for food resources and predator avoidance, especially in disturbed landscapes (Bergerud 1972, Chubbs et al. 1993, Mahoney and Virgl 2003). Movement is minimal during this season (Mahoney and Schaefer 2002a); resulting in relatively small ranges (Mahoney and Virgl 2003).

Caribou calf predators in this region include coyotes (*Canis latrans*), black bears (*Ursus americanus*), lynx (*Lynx canadensis*), and bald eagles (*Haliaeetus leucocephalus*). Wolves (*Canis lupus*) were once present on the island but were extirpated around 1922

(Allen and Barbour 1937). Sixty-three years later, the canine threat returned with the coyote's range expansion into Newfoundland (Mahoney and Schaefer 2002a). Moose (*Alces americanus*) were introduced to the island and have reached densities of four individuals/km^2 (McLaren et al. 2004). Licensed caribou hunting is open from September to December except within the Grey River management zone (Fig.1). Clear-cut forest harvesting has been ongoing since the 1920's in the west, and has spread across the interior.

Data Collection

Between 2005 and 2008, 104 adult female caribou were captured from helicopters using either Carfentanil citrate darting (3mg/ml Carfentanil at 25µg/kg reversed with 50mg/ml Neltrexone at 2500µg/kg; Canadian Association of Zoo and Wildlife Veterinarians 2009), or net gunning, and fitted with Argos Satellite collars (Lotek Engineering Systems, Newmarket, Ontario, Canada). Collaring took place during winter months when snow made caribou easier to locate and capture. Health Canada approved the capture and collaring protocol under experimental studies certificates 60021 and 60022. The collars were scheduled to record locations every 4 days. Locations recorded between June 1st and October 31st were chosen to represent the CPCR. To reduce error and maximize the number of relocations, only records with error margins of class 2 (<500m) or 3 (<250m) were used (Lotek Engineering Systems, Newmarket, Ontario, Canada). These 6557 locations (32 ± 7.26 female/herd/year ± SE), belonging to an average of 9 ± 1.30 females per herd/year ± SE, were mapped using ArcGIS 9.3 Geographic Information System (ESRI Inc., Redlands, California).

The annual CPCRs of collared females were then calculated as the 95% Minimum Convex Polygon (MCP; Mohr 1947) using the Home Range extension for ArcGIS 9.3 (Rodgers et al. 2007). This estimator was used because Stuart-Smith et al. (1997) found the minimum number of locations required for multi-year home range identification by 100% MCP to asymptote at 37 locations. This number is slightly higher than our average 32 ± 7.26 locations, but it was established for calculating the yearly home range over several years, rather than half the home range yearly. Additionally, Schaefer and Mahoney (2007) studied habitat selection at different scales, one of which was individual caribou's yearly MCPs created with $\geq$7 locations. Caribou habitat selection was found to be strongest at this scale. CPCR landscape component values for all females were averaged annually by herd, possibly resulting in a bias for CPCRs belonging to females with more re-locations (Johnson and Gillingham 2008).

A disturbance factor was considered to be any anthropogenic or natural factor affecting the landscape that had been associated with caribou avoidance, population decline, or increased predation. From the literature, nine disturbance factors were identified (Table 1). Yearly maps for each factor were obtained from several sources with varying accuracies. In cases where no new information was available for a disturbance factor, the previous year's map was used. Disturbance factors were mapped in ArcGIS 9.3 (ESRI Inc., Redlands, California). Human-generated disturbances were given a 250m avoidance buffer while forest fires were left un-buffered (Sorensen et al. 2008). Caribou have been documented to avoid roads by up to 250m (Dyer et al. 2001), and cut blocks by 1.2km (Smith et al. 2000) and 10.2km (Chubbs et al. 1993), so a 250m avoidance buffer was considered a conservative approach. A total disturbance layer was then created by simply merging and dissolving the buffered yearly disturbances to remove any overlap between them. The area of each female's yearly CPCR occupied by this total disturbance layer was extracted in ArcGIS 9.3 (ESRI Inc., Redlands, California) and averaged annually for each herd. From preliminary analyses, the total disturbance layer covered an average of 11.0% of CPCRs, and was composed of 40.9% roads, 37.3% logged areas, 10.3% fires, 5.4% power lines, and 6.2% other (agriculture, cabins, railway, drilling holes and quarries).

To determine the landcover types available to each caribou herd, we used raster classified LANDSAT-7 images (25-m pixels) from 2000 (Earth Observation for Sustainable Development of forests; ca. 80% pixel identification accuracy; Wulder et al. 2007). EOSD data labelled 25×25-m cells as primarily composed of one of 19 landcover types, which we reduced to 11 landcover types by combining the different density classes of the same vegetation types. The total area of each female's yearly CPCR occupied by the landcover types were extracted in ArcGIS 9.3 (ESRI Inc., Redlands, California) and then averaged annually for each herd. From preliminary analyses, CPCRs were composed of an average of 31.3% coniferous forest, 15.4% wetlands, 13.7% barren ground, 10.8% shrub land, 10.1% water, and 7.9% other (deciduous forest, herbs, mixed forest, snow, rock, shadow, or no data).

We used calf recruitment rates derived from fall classification surveys to examine the relationship between disturbance and population declines. Classifications were conducted within areas known to be occupied by each of the six herds during October or November of 2005 to 2008 by helicopter (Eurocopter AS350 Ecureuil or 206 Long Ranger). The crew included the pilot and two observers. A meandering flight path was followed in order to cover as much open habitat as possible, with the assumption that population structures of caribou found in these open habitats were representative of the entire population. Caribou were identified as adult/yearling/calf based on a combination of the relative body size; face length and antler presence/size, while adult females were differentiated from adult males based on the presence of a vulva patch. Calf recruitment was expressed as the number of calves per 100 adult females in late fall (Mahoney and Schaefer 2002a, Mahoney and Virgl 2003, Schaefer and Mahoney 2007). No classification data was available for the Grey River herd in 2005, the Mount Peyton herd in 2005, or the LaPoile herd in 2006, giving a sample size of 21 herd/year combinations.

Statistical Analysis

We first used general linear models (Proc GLM in SAS 9.1; SAS Institute Inc. Cary, NC, USA) to assess how calf recruitment, CPCR size and total disturbance area varied between herds and years. Linear mixed models (Proc MIXED in SAS 9.1; SAS Institute Inc. Cary, NC, USA) were used to examine the relationship between calf recruitment and total disturbance area or landcover type, between total disturbance and CPCR size, as well as between the number of radio-relocations and CPCR size. Possible herd effect was controlled for by including herd as a categorical fixed variable in the mixed models. Because our data were from several herds being measured within the same year, we included "year" as a random term in our models to avoid pseudo-replication. Finally, we searched for the best model to explain change in calf recruitment that included both total disturbance area and some landcover parameters, using an information-theoretic approach (Akaike 1973, Burnham and Anderson 2002, Stephens at al. 2005). This was done using linear mixed model analyses (Proc MIXED in SAS 9.1; SAS Institute Inc. Cary, NC, USA) and models included herd, total disturbance area and 1-2 of five landcover variables chosen based on findings from habitat selection literature. We restricted ourselves to models with five or fewer terms to avoid over-parameterization of the models (Quinn and Keough 2002). Models were evaluated based on their Akaike's Information Corrected Criterion (AIC_c) weight values and we report only those models with AIC_c weights > 0. For the sake of pluralism and because we were also interested in effect size and parameter precision, we report parameter estimates and their accompanying *P* values (Stephens et al. 2005) for models not distinguishable from the best model (i.e. ΔAICc < 2). A *P* value < 0.05 was used to denote statistical significance.

Results

Average calf recruitment differed significantly between the herds ($F_{5,15} = 7.92$, $P < 0.001$; Fig 2A), but not between years ($F_{3,17} = 0.81$, $P = 0.51$). Yearly calf recruitment ranged from 5.70 calves per 100 adult females in Pot Hill herd up to 26.58 calves per 100 adult females in the Buchans herd.

Average CPCR area differed significantly between the herds ($F_{5,15} = 8.86$, $P < 0.001$; Fig 2B), but did not differ between years ($F_{3,17} = 0.59$, $P = 0.63$). Females belonging to the Gaff Topsails and Buchans herds had CPCRs approximately 3.80 times larger than those from the Mount Peyton, Grey River, or Pot Hill herds; while females from the LaPoile herd had CPCRs 5.30 times larger. CPCR size was not significantly dependent upon the number of radio relocations ($F_{3,11} = 0.12$, $P = 0.74$).

Average total disturbance area within CPCRs differed significantly between herds ($F_{5,15} = 6.99$, $P = 0.002$; Fig 2C) ranging from 0.6% of the total CPCR area for the LaPoile herd to 36.9% of the total CPCR area for the Mt. Peyton herd. Total disturbance area did not vary between years ($F_{3,17}$ = 0.06, P = 0.98).

CPCR size was significantly ($F_{3,11}$ = 24.14, P < 0.001) related to disturbance level, such that when controlling for herd, CPCR size increased by an average 5.40 km^2 (SE = 1.18) for every additional km^2 of disturbed area (Fig 3A). CPCRs of collared females had an average overlap of 32.05 ± 25.35% within herds.

A significant negative relationship ($F_{3,11}$ = 7.21, P = 0.02) occurred between total disturbance area (km^2) and calf recruitment (b = - 0.05, SE = 0.02; Fig 3B). Of the eleven natural landcover types, mixed forest area (km^2) was the only one that was significantly related to calf recruitment, the relationship being negative (b = - 0.35, SE = 0.14, $F_{3,11}$ = 6.08, P = 0.03).

When total disturbance area was combined with the chosen landcover variables (barrens, coniferous forest, deciduous forest, mixed forest, and wetlands) in linear mixed models controlling for herd, AIC$_c$ weights revealed a confidence set of 12 candidate models, i.e. models with AICc weight > 0 (Table 2). The top model included, in addition to random effect of herd, a negative effect of total disturbance area (b = - 0.05, SE = 0.02) and a negative effect of deciduous forest (b = - 0.13, SE = 0.26), and was only 1.11 times more likely than the second ranked model. Plotting observed calf recruitment vs. calf recruitment as predicted by the top model gave an R^2 value of 0.81 (Fig 4). The most prominent landcover variables among the models with ΔAIC$_c$ < 2 were deciduous and mixed forest, with the latter showing the expected negative, but non-significant trend with calf recruitment (b = - 0.14, SE = 0.21). Barrens and wetlands were also within

$\Delta AIC_c < 2$. displaying the expected positive trend with calf recruitment ($b = 0.05$, SE = 0.02 and $b = 0.07$. SE =0.03 respectively).

Discussion

In general, caribou populations with greater than 15% young in the total population (at 6 - 10 months after calving) are expected to be in growth phase (under low hunting pressures) (Bergerud 1992). Converting our calf recruitment data to percent young by including adult males and yearlings in the ratio gives an average of 12% young in the total population, with a minimum and maximum value of 5.45 and 20.81% respectfully. This result supports speculations that woodland caribou population declines are due to poor calf recruitment. Although calf recruitment was low, percent disturbances for Newfoundland herds (average 10.95%) were comparatively smaller than those found in Northern Alberta (average 54.2% industrial and 22.1% fire disturbance within herd's ranges, with 2/6 herds not in decline; Sorensen et al. 2008). Fragmentation patterns may be an additional important factor contributing to Newfoundland caribou population declines (Dyer et al. 2001, Hins et al. 2009), where disturbances may be dispersed in Central Newfoundland and more clumped in Northern Alberta.

The CPCR sizes were statistically different between herds, with the Lapoile herd, found in the south east, covering the largest area. Acquisition of high quality habitats may be driving this difference, since Lapoile's CPCRs had approximately 14% less coniferous forest than the other herd's CPCRs. CPCR size also varied according to disturbance levels. While accounting for inter-herd differences, every additional km^2 of total disturbance within female's CPCRs, we saw an expansion of 5.40 km^2. Courtois et al. (2007) also found caribou range size to increase from 224 to 1198 km^2 as disturbance climbed from 0 to 40%, but size declined again at disturbance levels greater than 40%. Disturbance levels in our study were always below 40%. Assuming similar movement paths, larger ranges could lead to more travel time and hence higher energy expenditure (Bradshaw et al. 1997). Increased movement has also been suggested to increase calf predation risk for woodland caribou, as movement can decrease the effectiveness of the 'space-out' antipredator strategy (Harrington 2001, Gustine et al. 2006).

The relationship between the total disturbance and calf recruitment shows promise as a useful conservation management tool for Newfoundland populations. Contrary to Sorensen et al.'s (2008) findings that caribou populations should be in a growth phase if year-round home ranges contain less than 61% industrial footprint or 66% burnt areas, our populations contained a maximum of 36.85% disturbed areas during the more sensitive calving/post-calving season, but were in decline. In Quebec, Courtois et al. (2007) found no difference between calf recruitment in undisturbed and disturbed landscapes (areas within 500m of recent cuts, burns, regeneration sites, lichen-less heath, hardwood or mixed forest stands). From this study, herd calf recruitment was expected to decrease by 1 with every additional $20km^2$ of total disturbance within female's CPCRs. Caution must be exercised when extrapolating such correlative study results for management of local populations, as the mechanisms behind such relationships are not often known or understood, and can vary between herds.

Deciduous and mixed forests were both highly selected for among the most likely AIC_c-based models and had a negative relationship with recruitment. Wittmer et al. (2007) found survival of adult female mountain caribou to decrease with increasing mid-seral forest stands in British Columbia. Regenerating forest stands have also been found to be preferentially selected by coyotes in Eastern Quebec (Boisjoly et al. 2010), who are major calf predators in Newfoundland. Barrens and wetlands' positive trends with recruitment can be supported by Mahoney and Virgl (2003), Schaefer and Mahoney (2007), and Hins et al. (2009), who found these landcover types to be preferred by woodland caribou. In general, females tend to use a variety of habitats during summer with an emphasis on coniferous forests (Chubbs et al. 1993). Although coniferous forest was not among the variables found in the top AIC models, it was a preferred landcover type in Newfoundland (Schaefer and Mahoney 2007), was related to adult female survival in BC (Wittmer et al. 2007) and is important for calf predator refuge (Bergerud 1972).

Although the mechanisms through which disturbances are related to calf recruitment are not clearly understood, there are several plausible and connected theories in the literature. Caribou disturbance avoidance can create functional habitat loss and limited forage availability, leading to slower female growth and fat accumulation (Nellemann et al. 2000, Vistnes et al. 2001), lower pregnancy rates (Thomas 1982), lighter calf birth weights, slower calf growth rates, and poor calf recruitment (Weladji and Forbes 2002, Cameron et al. 2005). Disturbance avoidance can also lead to density increases (Nellemann and Cameron 1996), which can break down the woodland caribou antipredator tactic of dispersing or 'spacing out' during calving (Bergerud et al. 1990). Disturbances tend to create pockets of early successional forests (Carleton and MacLennan 1994, Hins et al. 2009), which are not suitable for caribou (Rettie and Messier 2000, James et al. 2004), but are favoured by other prey species, such as moose (Laliberte and Ripple 2004) and their predators (Boisjoly et al. 2010). These predators (wolves) have been found to spill over into caribou habitat to make use of this alternative prey in Alberta, BC, and Ontario (Seip 1992, Cumming et al. 1996, James et al. 2004). In Newfoundland, there are no wolves, but existing caribou predators are known to prey upon moose calves (Mahoney and Virgl 2003) and could be benefitting from habitat disturbances. Additionally, linear features such as power lines or roads can provide lower resistance travel routes for these predator populations (Edmonds and Bloomfield 1984), creating higher predator success rates (James and Stuart-Smith 2000).

Management Implications

Protection of calves within their CPCR appears to be the best way to encourage woodland caribou population persistence in Newfoundland. Total disturbance area has been highlighted as an important measure and management tool to relate calf survival to human industry. Disturbance sources should be limited within CPCRs, however when this is inevitable, our landcover results may be helpful. We believe that an increase in deciduous or mixed forest landcover during disturbance recovery may be linked to increased predation risk for calves, therefore directly affecting calf recruitment. Alternatively, the positive relationship of barrens and wetlands to calf recruitment shows that these landcover types are favourable for maintaining sustainable woodland caribou populations. We recommend conservation of coniferous forests around CPCRs and when disturbance must be implemented that: 1) disturbance sources be clumped together to reduce the combined footprint and 2) logged or mined areas be planted with coniferous seedlings to accelerate regeneration to climax forest stages post industry. In coming years, with additional data and an improved model, we may be able to identify a disturbance threshold at which recruitment rates fall below sustainable levels. In the meantime, these findings should inform managers in evaluating the consequences of further industrial development on habitat availability, predation risk, and calf recruitment for this region.

Table 1: Disturbance factors found to impact caribou, references, their main finding, sources of the files used to map each factor and their estimated accuracies (m).

Disturbance Factor	Reference	Documented Effect	Map Source	Accuracy
Agricultural Land	(Apps and McLellan 2006)	Negative association with caribou persistence	Department of Natural Resources, Forestry Division, Gov. NL.	<20
Recreation Facilities	(Dumont 1993, Nellemann et al. 2000, Forbes et al. 2001, Nellemann et al. 2001)	Reduced time feeding, Increased densities in non-disturbed areas, Reduced forage availability, Population fragmentation	Department of Environment and Conservation, Crown Lands Division, Gov. NL.	<50
Cutovers	(Chubbs et al. 1993, Smith et al. 2000, Schaefer and Mahoney 2007, Hins et al. 2009)	Used less than expected, Avoided by 1.2km, Avoided by females by 9.2km, Used less than expected.	Department of Natural Resources, Forestry Division, Gov. NL.	<20
Exploratory Drilling	(Bradshaw et al. 1997, Bradshaw et al. 1998)	Reduction in body mass, Displacement	Department of Natural Resources, Geological Survey of NL, Gov. NL.	<100
Fires > 200ha	(Chubbs et al. 1993, Rettie and Messier 2000, Dunford et al. 2006, Gustine and Parker 2008, Sorensen et al. 2008)	Used less than expected, Avoided, Reduced lichen abundance, Avoided, Negative effect on population growth	Canadian Large Fire Database 2009, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta.	Unknown
Power Lines	(Vistnes et al. 2001, Nellemann et al. 2003, Apps and McLellan 2006)	Increase densities in non-disturbed areas, Decrease in density around power lines, Negative association with caribou persistence	Newfoundland and Labrador Hydro	Unknown
Quarries	(Weir et al. 2007)	Displacement up to 4km and reduced group size within 6km	Quarry Management System, Dept. of Natural Resources, Mineral Lands Division. Gov.NL.	<10
Railways	(Nellemann et al. 2001, Simpson and Terry 2003, Apps and McLellan 2006)	Population fragmentation, Displacement, Negative association with caribou persistence	Dept of Environment and Conservation, Parks and Natural Areas Division. Gov. NL.	GPS <2 CanVex <100
Roads	(Schindler et al 2007, Nellemann and Cameron 1996, James and Stuart-Smith 2000, Dyer et al. 2001, Vistnes et al. 2001, Nellemann et al. 2001, Cameron et al. 2005, Apps and McLellan 2006)	Loss of quality habitat within 1km of roads, Decrease use within 4km or roads, Elevated predation, Decreased habitat use within 500m of roads, Increased density in non-disturbed area, Decreased density close to roads, Population fragmentation, Displacement and population split, Negative effect on caribou persistence	Geobase®, National Road Network. Dept Environment and Conservation, Forestry Division, Gov. NL.	<10

Table 2: AIC_c, delta AIC_c, and AIC_c weights of models containing a combination of total disturbance and natural landcover area variables. Abbreviations: Dist = Total Disturbance, Barr = Barrens, Coni = Coniferous Forest, Decid = Deciduous Forest, Mixed = Mixed Forest, and Wet = Wetlands. All other model combinations had more terms and/or a lower AICc and are therefore not included.

Model	**AIC_c**	**ΔAIC_c**	**$AIC_c\omega$**
Dist + Decid	93.80	0.00	0.15
Dist + Mixed	94.00	0.20	0.14
Dist + Decid + Mixed	94.00	0.20	0.14
Dist + Mixed + Wet	94.60	0.80	0.10
Dist + Decid + Barr	94.70	0.90	0.10
Dist + Mixed + Barr	94.90	1.10	0.09
Dist + Barr	95.50	1.70	0.07
Dist + Coni	96.10	2.30	0.05
Dist + Decid + Wet	96.50	2.70	0.04
Dist + Wet	96.90	3.10	0.03
Dist + Coni + Decid	97.20	3.40	0.03
Dist + Coni + Mixed	97.50	3.70	0.02

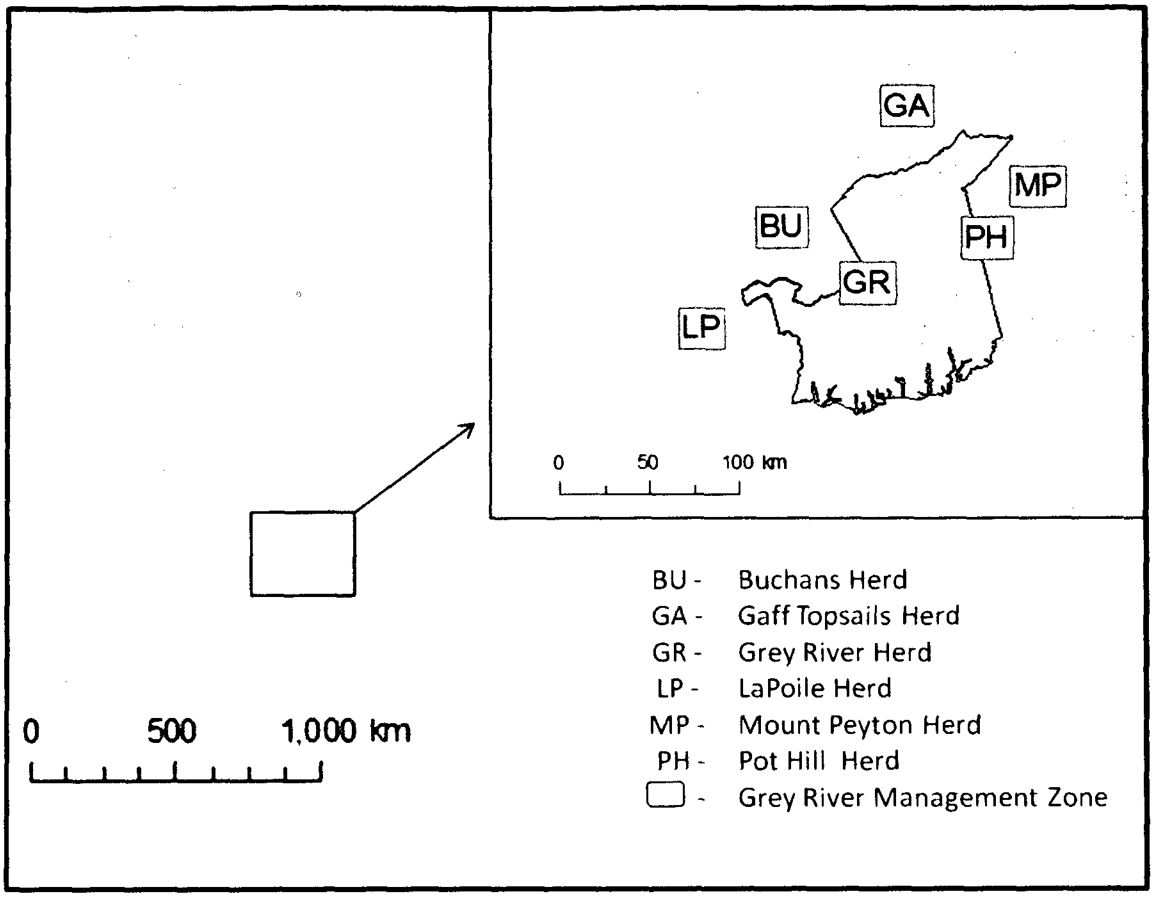

Figure 1: Study area in central Newfoundland, Canada. Inset shows general location of the female calving/post calving range of six study caribou herds from 2005-2008. Outlined region in the inset represents the Grey River Management Zone, within which caribou hunting is prohibited.

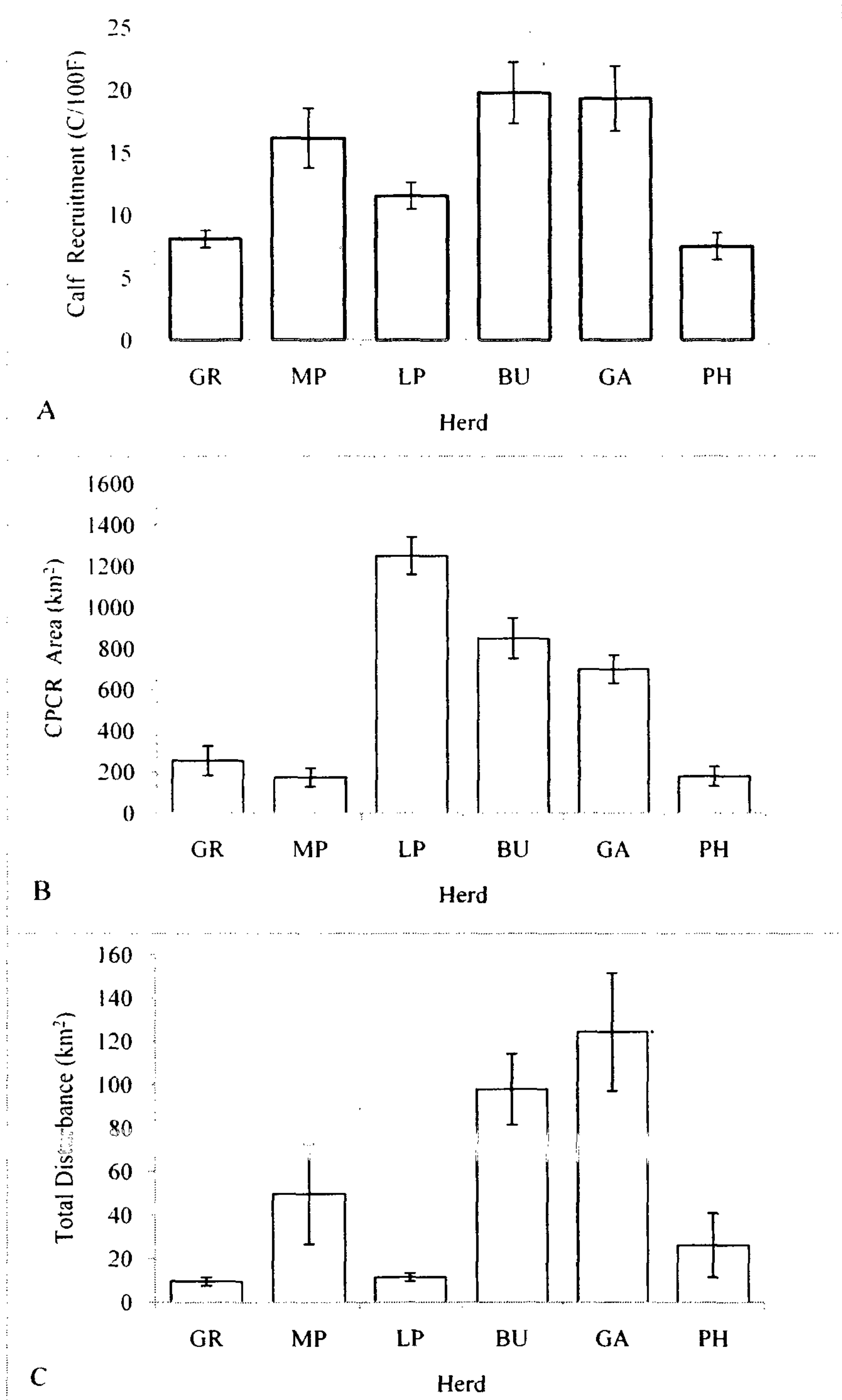

Figure 2: Difference between caribou herds in respect to average yearly (A) calf recruitment (calves/100 adult females), (B) female's CPCR size (km^2) and, (C) total disturbance area (km^2), from 2005-2008 in Newfoundland, Canada. Error bars are 1 SE of the mean. Abbreviations for herds: GR = Grey River, MP = Mount Peyton, LP= LaPoile, BU = Buchans, GA = Gaff Topsails, and PH = Pot Hill.

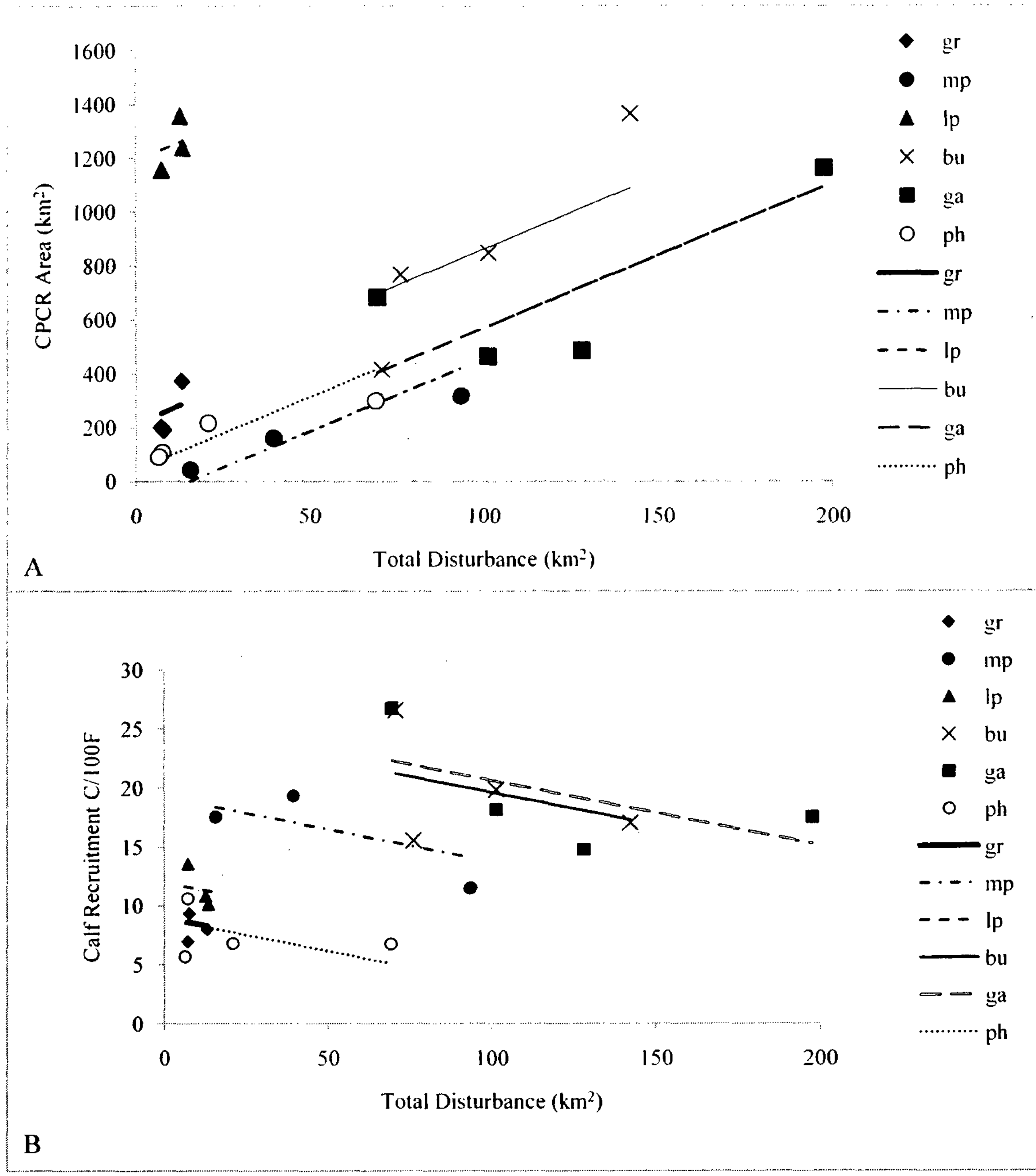

Figure 3: Relationship between total disturbance area (km^2) and (A) the average female CPCR size (km^2) and (B) calf recruitment (calves/100 adult females) from 2005-2008 in Newfoundland, Canada. Abbreviations for herds: gr = Grey River, mp = Mount Peyton, lp= LaPoile, bu = Buchans, ga = Gaff Topsails, and ph = Pot Hill.

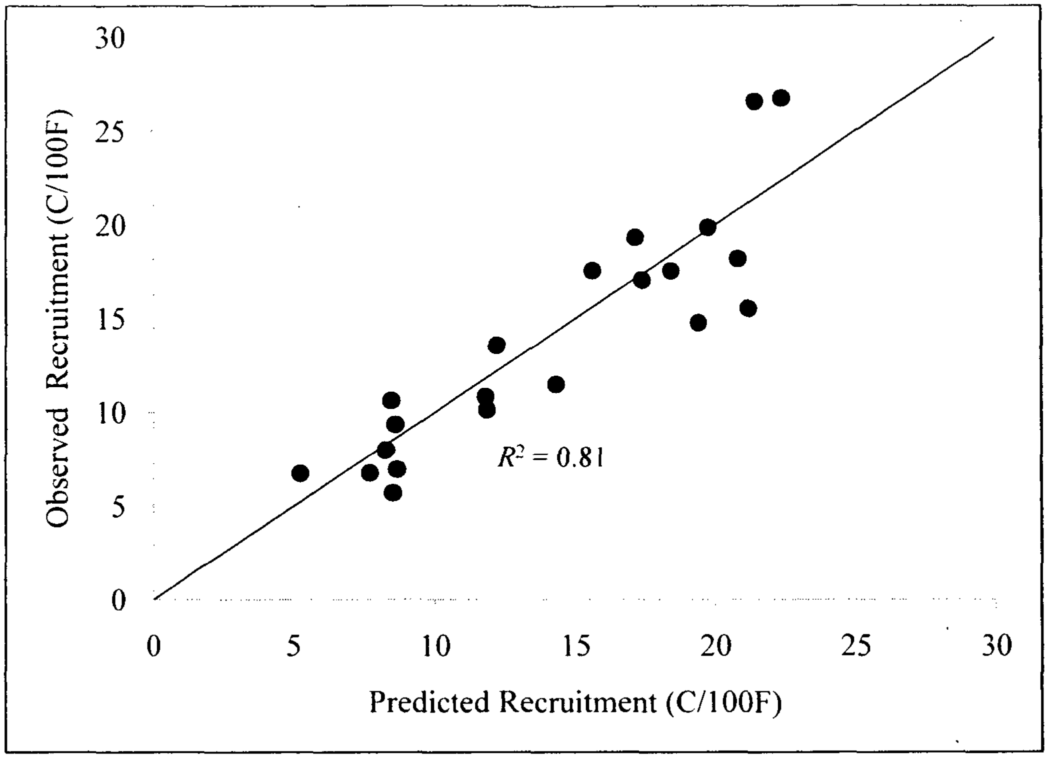

Figure 4: Observed calf recruitment (calves/100 females) from 2005-2008 in Newfoundland, Canada, versus calf recruitment (calves/100 females) as predicted by top AIC_c ranked linear mixed model (accounting for herd) with year as a random term; recruitment = herd + total disturbance + deciduous forest. The line represents where the points would lie if the model fit the observed calf recruitment perfectly.

Chapter 2:

Influence of Landscape Fragmentation on Woodland Caribou Calf Recruitment

Sara, C. McCarthy[1], Robert B. Weladji[1], Christine Doucet[2], and Paul Saunders[2]

[1] Department of Biology, Concordia University, 7141 Sherbrooke Street W., Montreal, QC, H4B 1R6, Canada

[2] Wildlife Division, Newfoundland and Labrador Department of Environment and Conservation, 117 Riverside Drive, P. O. Box 2007, Corner Brook, NL, A2H 7S1,

Abstract

The effects of landscape fragmentation on wildlife are considered to be less severe than those of habitat loss. This may be a product of using fragmentation measures of little biological relevance, as well as a lack of separation between habitat loss and fragmentation in study design. Caribou populations seem to be especially sensitive to landscape fragmentation because it degrades their 'space-out' predator avoidance strategy and increases their predation risk. Predation has brought calf survivorship rates as low as 3% in Newfoundland, and thus, habitat selection should occur at a coarse spatial scale based on this limiting factor. In Chapter 1 we found that disturbance area and natural landcover type explained some of the variation in calf recruitment. As a follow up from this finding, and given the potential role of configuration, we examined whether accounting for fragmentation would improve our ability to explain variation in calf recruitment, using an information theoretic approach. We created a digital map of fragmenting factors and measured its configuration within the calving/post-calving ranges (CPCR) of female caribou. We used three different measures of fragmentation (effective mesh size, edge to area ratio, and fragmentation extent), and assessed their influence on calf recruitment. We found that the fragmentation measures differed in their quantification of CPCR configuration, and that none of these measures alone were significantly related to calf recruitment. However, the addition of *edge to area ratio* to our previous models of calf recruitment resulted in a considerable decrease in AIC_c values and hence ameliorated models. The most parsimonious model included the effect of edge to area ratio, total disturbance area, mixed forest area, and wetland area, suggesting fragmentation to be important for the variation in woodland caribou calf

recruitment. We stress the importance of exploring fragmentation irrespective of habitat loss, of using multiple measures of fragmentation, and the cumulative nature of landscape disturbance. CPCR fragmentation by disturbed landscapes appears to be an important aspect to consider for caribou conservation.

Introduction

Landscape disturbance and the associated effects of habitat loss and fragmentation on wildlife behaviour, movement, resource selection, reproduction, and/or survival have been a central focus for conservation biologists and landscape ecologists (Jalkotzy et al. 1997, Theobald et al. 1997, Fahrig 2003, Johnson et al. 2004, Jaeger et al. 2005, St-Laurent et al. 2009). In general, landscape fragmentation has been considered of less importance when compared to the substantial negative effects of habitat loss (Fahrig 2003). This may be due to the lack of a consistent definition for fragmentation, as well as the lack of separation between the effects of habitat loss and fragmentation in study design (Fahrig 2003).

Despite having modest biological significance in comparison with habitat loss, landscape fragmentation has been negatively associated with several wildlife population traits, including body condition, abundance, mortality, movement, predation, reproduction, genetic diversity, and community composition (Oehler and Livaitis 1996, Chan-McLeod et al. 1999, Zollner and Lima 1999, Calabrese and Fagan 2004, Eigenbrod et al. 2008, St-Laurent et al. 2009). For caribou (*Rangifer tarandus*), the most interesting and alarming effects of landscape fragmentation are related to predation. It is widely accepted that the proximate limiting factor for caribou populations is predation (Rettie and Messier 1998, Wittmer et al. 2005b). Woodland caribou (*R. t. caribou*) are particularly at risk when fragmentation degrades their 'space-out' strategy to minimize predation risk (Bergerud et al. 1990, Harrington 2001, Gustine et al. 2006). Fragmentation can also increase predation rates when habitat types associated with fragmentation and disturbance proliferate, creating spatial overlap with other ungulate species and their associated predators (Mahoney and Virgl 2003, Wittmer et al. 2005b. Apps and McLellan 2006).

To further understand the consequences of disturbance levels on woodland caribou conservation, we must identify the relationships between landscape structure (composition and configuration) and vital rates (Sorensen et al. 2008, Vistnes and Nellemann 2008). Newfoundland woodland caribou populations have declined by an estimated 66% since the 1990s, possibly due to a severe drop in average calf survivorship (67% in the 1980s and 90s to approximately 3% from 2003-2007; Mahoney et al. 2008). In Chapter 1 we found that landscape composition, namely total disturbance area and deciduous/mixed forest areas were negatively related to calf recruitment rates (calves/100 adult females) in Newfoundland. However, total disturbance area was found to be covering a smaller percentage of female's calving/post-calving ranges (CPCRs) than expected with such a population decline (Sorensen et al. 2008). We then suggested that fragmentation patterns (landscape configuration) created by this disturbance area may be an additional factor to consider and that perhaps some of the variation in calf recruitment among these Newfoundland herds could be explained by variation in CPCR fragmentation.

Landscape fragmentation can simply be defined as the presence of barriers to wildlife movement (Chetkiewicz et al. 2006). More specifically, it is at least one of five processes affecting landscape patterns: reducing habitat quantity, increasing patchiness, decreasing patch size, increasing isolation, and increasing patch edge (Fahrig 2003). In this study, for sake of clarity and ease of separating effects of habitat loss and fragmentation, we will characterize landscape fragmentation as landscape configuration, which excludes habitat quantity from the definition. Using this basis, landscape fragmentation can be seen as the division of the landscape irrespective of habitat loss (Fahrig 2003).

Common approaches used to quantify functional landscape fragmentation require the landscape to be divided into habitat type patches (i.e. functional graph theory). This identification of habitat patches may create uncertainty and error as patches are not fixed elements of the landscape and should be defined relative to the species and question at hand (Turner et al. 2001). Even if an appropriate patch scale has been selected; the use of contiguity rules to define the patches creates additional problems, since the mapping cell size affects the outcome of patch size and shape (Girvetz and Greco 2007). Patches must also be assigned a resistance value according to the study species' habitat selection preference, which requires a great depth of information regarding the species' responses to habitats, disturbances, elevation, slope, ruggedness, and climate. Such methods can be informative, yet data intensive.

Simpler methods examine landscape fragmentation from a structural perspective, but still require the identification of the habitat patches within the landscape (i.e. number of patches, patch area, core area, patch perimeter, shape index, nearest neighbour). Although easier to calculate, such structural measures of landscape fragmentation have been criticized for their ambiguity and lack of biological relevance (Bender et al. 2003, Calabrese and Fagan 2004, Kindlmann and Burel 2008). A geometric approach called the effective mesh size (Jaeger 2000) has emerged as a possible intermediate metric that balances the benefits of functional and structural measures. This metric corresponds to the probability that two organisms can meet in the landscape without having to cross any disturbance barriers and is the only metric that characterizes fragmentation independently of CPCR size.

Our first objective was to explore the fragmentation level of female's CPCRs of six Newfoundland woodland caribou herds over four years (2005-2008) and investigate how these fragmentation levels relate to calf recruitment. We quantified landscape fragmentation as effective mesh size, as well as by two other measures based on disturbance perimeter (edge to area ratio), or distance of caribou to disturbance (fragmentation extent) while controlling for area. Finally, we added the fragmentation measures to the landscape composition models generated in Chapter 1 to in order to assess whether accounting for landscape configuration can improve our ability to explain variation in woodland caribou calf recruitment for Newfoundland herds.

Materials and Methods

Study Area

The six sedentary woodland caribou herds were located in central Newfoundland, on Canada's East coast (Fig 5). Home ranges within these herds are relatively small compared to migratory caribou (Bergerud 1996), but there is some degree of seasonal range overlap between herds. Herd population estimates from 2007 (Table 3) ranged from 648 to 5400 individuals. Newfoundland caribou prefer mature coniferous forest to meet their basic forage and predator avoidance needs (Bergerud 1972, Chubbs et al. 1993, Mahoney and Virgl 2003). Female's CPCRs in this area were composed of an average of 31.3% coniferous forest, 15.4% wetlands, 13.7% barren ground, 10.8% shrub land, 10.1% water, and 7.9% other (deciduous forest, herbs, mixed forest, snow, rock, shadow, or no data; Chapter 1 in this thesis). Balsam fir (*Abies balsamea*) could be found among spruce (*Picea mariana* and *Picea glauca*) dominated coniferous forests with moss covered floors (*Hylocomium spp.*) (Daaman 1983).

The remaining 11.0% of the female CPCRs was occupied by buffered fragmentation factors, consisting of 41.9% roads, 37.2% logged areas, 10.3% burnt areas, 5.4% power lines, 2.7% agriculture, 1.1% railway, 0.3% drilling holes, and 0.01% quarries (Chapter 1). Pulp and paper production using clear-cut harvesting techniques has been driving the Newfoundland forestry industry since the 1920's, accounting for the majority of the roads found within CPCRs.

Annual herd calf recruitment over the four years of study averaged (± SE) 13.97 ± 1.35 calves/100 females, and ranged from 5.70 in Pot Hill herd during 2006, up to 26.58 in the Buchans herd during 2008 (Chapter 1). No classification data was available for the Grey River herd in 2005, the Mount Peyton herd in 2005, or the LaPoile herd in 2006, giving a sample size of 21 herd/year combinations.

Newfoundland has generally cool summers and winters with annual precipitation varying between regions (<1000 mm). From June-October it is unlikely that this maritime climate would have any severe effects on calf recruitment. Heat and wind however, may affect insect disturbance levels, potentially affecting caribou energy budgets (Helle and Kojola 1994, Hagemoen and Reimers 2002, Weladji et al. 2003). Other threats to calf survival on the island include licensed hunting of adults (~1%, September to December) and predation by black bears (*Ursus americanus*), coyotes (*Canis latrans*), bald eagles (*Haliaeetus leucocephalus*), and lynx (*Lynx canadensis*).

Data Collection

Relating calf recruitment to fragmentation first required the identification of areas occupied by females and calves of each herd during the calving/post calving season. This was done using Argos Satellite collars (Lotek Engineering Systems, Newmarket, Ontario, Canada) placed on 104 female caribou belonging to the six herds (9 ± 1.30 females/herd/year ± SE). Complete details for the collaring and location data filtration methods were reported in Chapter 1. These methods resulted in a data set of 6557 locations (32 ± 7.26 female/herd/year ± SE), which were mapped using ArcGIS 9.3 Geographic Information System (ESRI Inc., Redlands, California).

Yearly locations from each female were then used to calculate 95% Minimum Convex Polygons (MCP; Mohr 1947) using the Home Range extension for ArcGIS 9.3 (Rodgers et al. 2007), which represented the yearly CPCRs for females. Determining at which scale to conduct a study is a crucial yet challenging issue facing landscape ecologists and conservation biologists examining fragmentation (Johnson et al. 2002, 2004). Scale can influence whether effects of habitat loss or fragmentation are found to be negative, positive, or are even detected (Vistnes and Nellemann 2008). Habitat selection has been explored in a hierarchical framework (Johnson 1980), such that the most limiting and hence highest priority factors drive selection at the coarsest scale, while those showing less potential for limiting fitness drive selection at progressively smaller scales. Accordingly, woodland caribou should select habitat best suited for predator avoidance at the coarsest (seasonal range), or CPCR scale (Rettie and Messier 2000, Hins et al. 2009).

From the literature, any landscape disturbance that had been found to affect caribou movement was considered a fragmentation factor (see Chapter 1 for references and their associated effects). Yearly digital maps were obtained for nine fragmentation factors (agriculture, recreation facilities, logging, exploratory drilling, fires, power lines, quarries, railways and roads) and projected in ArcGIS (ESRI Inc., Redlands, California). Following the methods of Sorensen et al. (2008), a 250m buffer was created around the fragmentation factors, excluding fires, to represent area functionally lost due to disturbance avoidance (Sorensen et al. 2008). This buffer size was chosen as a conservative approach, as avoidance buffers have been documented with distances as large as 1.2 km and 10.2 km (Smith et al. 2000 and Chubbs et al. 1993 respectively). All fragmentation factors were then merged and dissolved to create one total fragmentation layer. CPCRs were used to extract the fragmentation layer and these extracts were merged to their respective CPCR MCP polygons to create one polygon representing habitat area and fragmentation layer area for each female/year.

Fragmentation values were assigned to CPCR polygons using three different methods: effective mesh size, edge to area ratio and fragmentation extent. Effective mesh size was calculated using the Effective Mesh Size Landscape Fragmentation Metric for ArcGIS (Girvetz et al. 2008). Only the output from the cutting out procedure (Jaeger 2000) was recorded, as we were only interested in patterns of the fragmentation layer within CPCRs. This method takes the sum of the squared suitable habitat areas (H), divided by the total area of the CPCR polygon (A) (Fig 6A). Calf recruitment was expected to increase with increasing effective mesh size. The edge to area ratio metric was calculated as the fragmentation layers' perimeter (P) divided by the area of the fragmentation layer (F), all divided by the total area of the CPCR polygon (A) (Fig 6B). Calf recruitment was expected to decrease with increasing edge to area ratio values. The fragmentation extent metric was calculated as the inverse of the average distance of a female's relocation records to the fragmentation layer within her CPCR polygon (D) divided by the area of the fragmentation layer (F), all divided by the total area of the CPCR polygon (A) (Fig 6C). The inverse was used in order to accommodate instances where the distance to was zero; such that lower fragmentation extent values could represent less fragmentation. Calf recruitment was expected to decrease with increasing fragmentation extent values.

$$Effective\ Mesh\ Size = \frac{1}{A}\sum_{i=1}^{n} H_i^2$$

$$Edge\ to\ Area\ Ratio = \frac{P/F}{A}$$

$$Fragmentation\ Extent = \frac{A}{D/F}$$

Statistical Analysis

We used general linear models (Proc GLM in SAS 9.1 (SAS Institute Inc. Cary, NC, USA)) to assess how the three fragmentation metrics varied between herds and years. Linear mixed models (Proc MIXED in SAS 9.1 (SAS Institute Inc. Cary, NC, USA)) were used to assess the relationship between the fragmentation metrics and calf recruitment. We controlled for a possible herd effect by including herd as a categorical fixed variable in the mixed models. To avoid pseudo-replication we included "year" as a random term in our mixed models because our data was from several herds measured within the same years. Finally, we examined whether these fragmentation measures could be used to ameliorate the combined total disturbance and landcover models selected in Chapter 1. We added each of the fragmentation measures to the selected models and looked for improvement using an information-theoretic approach (Akaike 1973, Burnham and Anderson 2002). We considered models with the lowest Akaike's Information Corrected Criterion (AIC_c) score to be the most parsimonious, i.e. the best model providing an approximation for the information in the data (Burnham and Anderson 2002). Model amelioration was evaluated based on the difference in AICc between models from Chapter 1 and the same models when including one of the fragmentation measures, with a delta $AIC_c > 2$ suggesting improvement. For the sake of pluralism and because we were also interested in effect size and parameter precision, we reported parameter estimates and their accompanying standard errors (Stephens et al. 2005) for the most parsimonious model. A P value < 0.05 was used to indicate statistical significance.

Results

Average effective mesh size differed significantly between the herds ($F_{5,15} = 12.02$, $P < 0.001$; Fig 7A), but not between years ($F_{3,17} = 0.75$, $P = 0.54$). Yearly effective mesh size ranged from 2504 m^2 in the Mount Peyton herd to 133254 m^2 in the LaPoile herd. Average edge to area ratio did not differ significantly between the herds ($F_{5,15} = 0.72$, $P = 0.62$; Fig 7B) or between years ($F_{3,17} = 0.56$, $P = 0.65$). Average fragmentation extent differed significantly between the herds ($F_{5,15} = 3.11$ $P = 0.04$; Fig 7C), but not between years ($F_{3,17} = 0.37$, $P = 0.77$). Yearly fragmentation extent metric ranged from 0.13 m^3 in the Pot Hill herd to 116.37 m^3 in the Gaff Topsails herd.

Linear mixed model analyses showed no significant linear relationship between any of the fragmentation metrics and calf recruitment (Effective Mesh; $F_{3,11} = 2.19$, $P = 0.17$, Edge to area ratio; $F_{3,11} = 3.98$, $P = 0.07$, Fragmentation extent; $F_{3,11} = 3.05$, $P = 0.11$).

Indeed, when the fragmentation measures were used in an effort to ameliorate recruitment models from Chapter 1, edge to area ratio came out as the only measure whose addition resulted in more parsimonious models (Table 4). All of the top seven models improved with the addition of edge to area ratio by decreasing their AIC_c value by > 2, meaning the new models were more parsimonious. The new top model had an AIC_c value 11.2 points smaller than the previous top model. It included, in addition to the random effect of herd, a non-significant effect of the edge to area ratio metric ($F_{3,8} = 0.46$, $P = 0.52$), a negative effect of total disturbance area ($F_{3,8} = 8.99$, $P = 0.02$), a non-significant effect of mixed forest ($F_{3,8} = 1.72$, $P = 0.23$), and a positive effect of wetlands ($F_{3,8} = 10.43$, $P = 0.01$). The R^2 value between calf recruitment as predicted by the new top model and calf recruitment as observed was 0.89 (Fig 8). The addition of effective mesh size or fragmentation extent measures to the top models had a negligible or negative effect on model performance as measured by AIC_c (i.e. delta $AIC_c < 2$).

Discussion

Using simple linear mixed models we found no significant relationship between measures of fragmentation and woodland caribou calf recruitment. Our ability to compare this finding to other research is limited, as the effects of landscape fragmentation irrespective of habitat loss on caribou vital rates have rarely been studied and have never been studied using the same fragmentation measures. This could be because of the difficulty in defining and measuring fragmentation without habitat loss, as well as because of the difficulty involved in making conclusions regarding vital rates for such a long-lived and wide-ranging species. Using the mean patch size, patch size coefficient of variation, largest patch index and interspersion, and juxtaposition index, Stuart-Smith et al. (1997) found that the more fragmented lansdscape had a lower percentage of females caribou with calves (10.0%) compared to the less fragmented one (28.3%) in 1994, but found no difference in 1995. Higher caribou mortality was recorded in an area with a higher average center versus neighbours' fragmentation index after forest harvesting (Kinley and Apps 2001). Female roe deer were found to have higher lifetime reproductive success in areas with lower road densities (McLoughlin et al. 2007), but this measure does not account for area and hence findings may be confounded by habitat loss. Our results support findings that habitat composition is relatively more important than configuration at coarse scales (Johnson et al. 2002, Wittmer et al. 2007). At finer spatial scales however, configuration of disturbance sources and their associated habitat types may affect predation risk of woodland caribou (Apps and McLellan 2006).

In spite of this lack of significance, one of the fragmentation measures (edge to area ratio) was found to substantially improve the selected models for calf recruitment from Chapter 1. Inclusion of edge to area ratio in our models decreased the top AIC_c value from 93.8 to 82.6, an improvement of 11.2 points; and the best-fitted model to our data included the effect of edge to area ratio, total disturbance area, mixed forest, and wetlands. Although relative importance of fragmentation effects have been low, their relevance in explaining calf recruitment was expected, based on the detrimental effects of linear features to caribou ecology documented in other studies; higher mortality (James and Stuart-Smith 2000), avoidance of suitable habitat (Dyer et al. 2001), population fragmentation

(Cameron et al. 2005), and range shifts resulting in increased population densities (Shindler et al. 2006, Weir et al. 2007). More specifically, edge effects, which we measured using edge to area ratio, have been found to reduce lichen abundance (Rheault et al. 2003), be negatively related to female survival (Wittmer et al. 2007), and selected against for calving sites (Bergerud 1971). We can assume that by amalgamating fragmenting structures in space and time, we will eventually be amalgamating the negative effects to a point at which vital rates are affected (Cameron et al. 2005).

There was variation in the results delivered by the three methods of measuring CPCR fragmentation. We expected that highly fragmented CPCRs would have smaller effective mesh sizes. Using this tool, the LaPoile herd was found to have the lowest fragmentation level, while the Mount Peyton and Pot Hill herds were found to have the highest. We expected highly fragmented CPCRs to have larger edge to area ratio measures. Using this tool, the LaPoile herd was found to have lowest fragmentation level, while the Buchans, Mount Peyton and Pot Hill herds were found to have the highest. We expected that highly fragmented CPCRs would have larger fragmentation extent measures. Using this tool, the Gaff Topsails herd had the highest level of fragmentation, and all other herds were comparatively less fragmented. Although the effective mesh size and edge to area ratio measures had similar trends, the fragmentation extent index gave a different outcome for fragmentation level ranking. The fragmentation extent measure was meant to be a functional measure of habitat fragmentation, as it reflects the adult female caribou's ability to avoid the fragmenting area. High fragmentation extent measures should signify a fragmentation pattern that is so dispersed that females cannot separate themselves spatially from the disturbance source. This variation in results between configuration tools is a good example of how different measures of fragmentation can give entirely different and perhaps biologically irrelevant results. There is no known measure that can describe all features and behaviours of landscape fragmentation (Davidson 1998). Tools used to analyze fragmentation patterns must be chosen specifically for the species, scale, ecosystem, and research question. It may in fact be necessary to use several measures of fragmentation in order to get an approximate description of the processes at hand (Hansen et al. 2001).

Our analysis of the direct relationship between fragmentation measures and calf recruitment may have had several inherent issues, perhaps explaining the lack of significant relationships. A close analysis of Figure 5 and the habitat loss data from Chapter 1 reveals that the majority of fragmentation was due to forestry operations and their associated roadways. This means that other than the three large clumped disturbance areas (forest fires), the fragmentation patterns were similar across herds, varying only in their intensity. This resulted in a relatively small range of fragmentation values that were perhaps not extreme enough to capture significant effects. The difficulty in performing experimental studies with such a long-lived and wide roaming species makes such issues inevitable. Secondly, all disturbance factors (roads, logged areas, burnt areas, power lines, agriculture, railway, drilling holes, and quarries), were given the same weight when considered as components of the fragmentation layer. The analysis could be improved by adding a degree of permeability to the different fragmenting factors (Jaeger et al. 2007), as not all of these factors would have had the same effect on the ecology of the caribou, nor on the ecology of their predators (Dyer et al. 2001, Lindenmayer and Franklin 2002). This would first require a comparison of the effects of each disturbance type on caribou ecology. Finally, because we were studying disturbance related fragmentation, water bodies were not included as a part of the fragmentation layer, although their configuration, depth, and width may have contributed to landscape fragmentation (Apps and McLellan 2006).

Management Implications

This study highlights the importance of separating the effects of habitat loss and landscape fragmentation. These processes can have different but synergistic effects on wildlife ecology, and these confounding effects may lead to erroneous conclusions if not accounted for separately. Although habitat loss has been shown to have a greater impact on caribou persistence, investigation of landscape fragmentation is still warranted. Habitat loss studies alone may report negligible losses when exploring landscapes with thin linear features branching across home ranges, when in fact these fragmenting structures may have large detrimental effects on caribou movement, resource use, reproduction, and survival. Consideration should also be given to the additive effects of the disturbance sources (natural and anthropogenic). The use of multiple measures of fragmentation should allow managers to weigh the costs/benefits of different industrial development or environmental rehabilitation patterns, in order to ensure the conservation of critical caribou habitat, the connectivity of those habitats, as well as spatial separation of caribou from disturbed landscapes and their associated predators. Using improved models, similar to those generated in this study, as well as a sustainable recruitment rate, maximum allowable fragmentation values could be calculated, and disturbance patterns for which that fragmentation value is not surpassed could be sought. In general, we recommend disturbances should be clumped as much as possible to limit fragmentation effects. The current pattern of forest harvesting not only constitutes habitat loss, but also affects caribou movement and increases predator access, subsequently affecting calf recruitment. New strategies would benefit from considering woodland caribou's 'space-out' calving survival tactic when implementing industrial disturbances.

Table 3: Population estimates ± 90% confidence intervals for the six study herds in 2007.

Data: Wildlife Division, Department of Environment and Conservation, NL.

Herd	Estimate	± CI
Buchans	4305	496
Gaff Topsails	2100	222
Grey River	1176	109.5
LaPoile	5400	537.5
Mount Peyton	648	43
Pot Hill	2950	268.5

Table 4: AIC_c values for recruitment models of similar parsimony ($\Delta AIC_c < 2$) presented in Chapter 1, followed by the AIC_c and delta AIC_c values (previous AIC_c – new AIC_c) of the same modes with an added fragmentation measure. Bolded numbers represent considerable improvements to AIC_c values ($\Delta AIC_c > 2$), while bolded model represent the new best fit model. (Barr = Barrens, Dist = Total Disturbance, Coni = Coniferous Forest, Decid = Deciduous Forest, Mixed = Mixed Forest, and Wet = Wetlands).

		Effective Mesh Size		*Edge to area ratio*		*Fragmentation extent*	
Model	AIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c	AIC_c	ΔAIC_c
Dist + Decid	93.8	111.4	-17.6	**84.7**	**9.1**	96.1	-2.3
Dist + Mixed	94.0	111.4	-17.4	**84.5**	**9.5**	97.2	-3.2
Dist + Decid + Mixed	94.0	107.7	-13.7	**83.1**	**10.9**	95.6	-1.6
Dist + Mixed + Wet	94.6	109.2	-14.6	**82.6**	**12.0**	94.5	0.1
Dist + Decid + Barr	94.7	110.7	-16.0	**84.1**	**10.6**	96.0	-1.3
Dist + Mixed + Barr	94.9	111.1	-16.2	**84.6**	**10.3**	97.0	-2.1
Dist + Barr	95.5	110.9	-15.4	**84.4**	**11.1**	96.9	-1.4

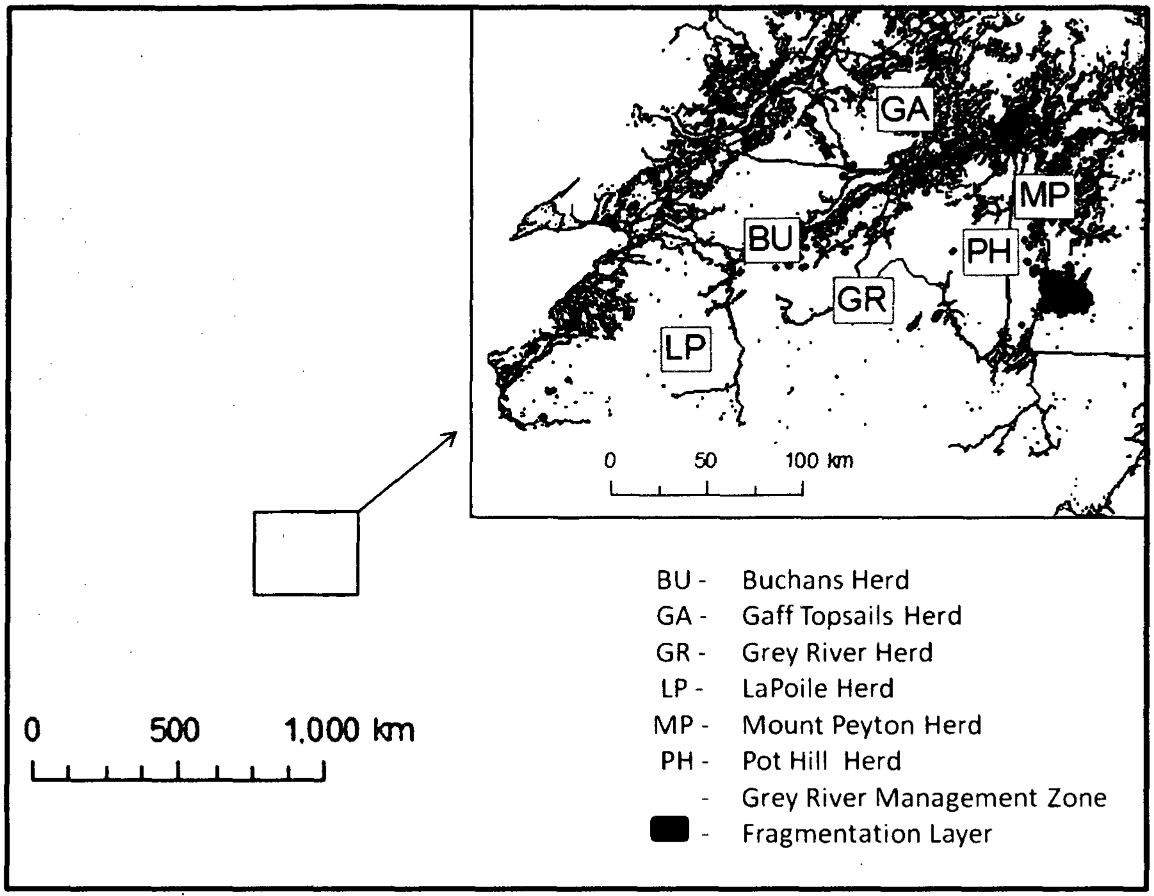

Figure 5: Study area in central Newfoundland, Canada. Inset shows all disturbance sources considered to be components of the fragmentation layer (black) that were mapped in 2008, as well as the general location of the female calving/post calving range of the six study caribou herds from 2005-2008. Outlined region in the inset represents the Grey River Management Zone, within which caribou hunting is prohibited.

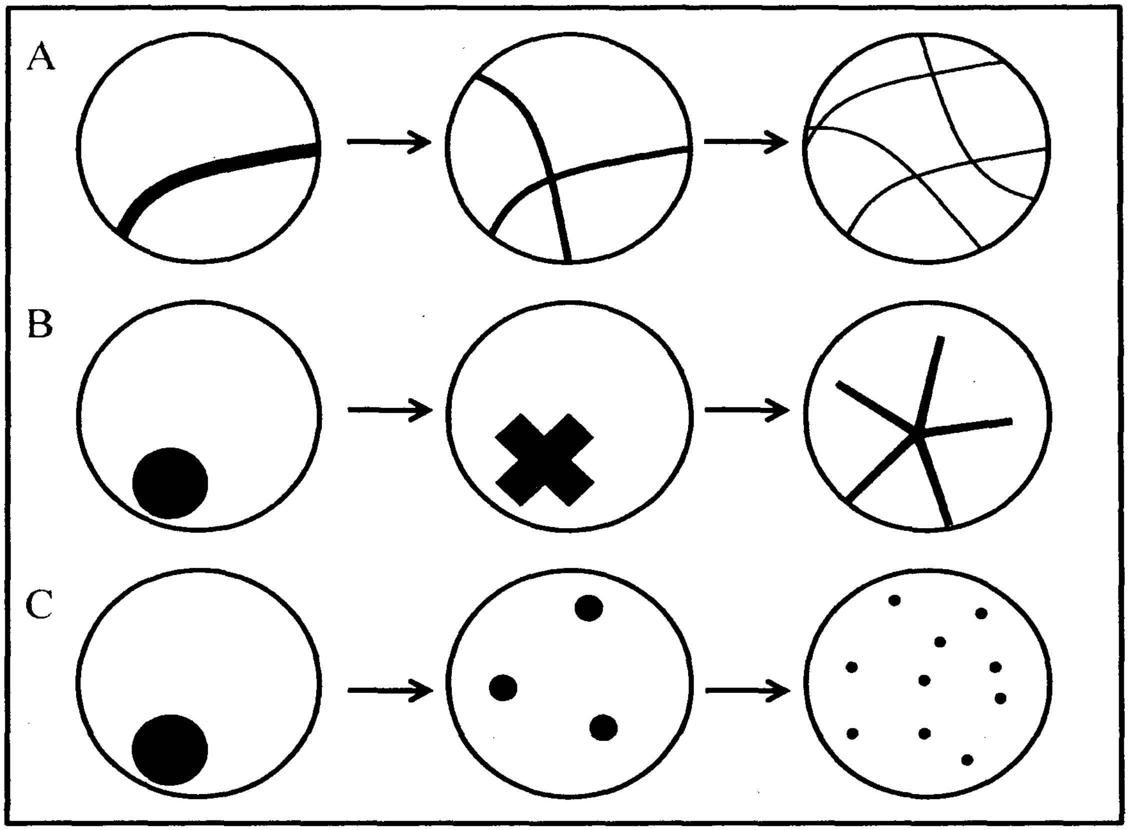

Figure 6: Illustration of how each of our three fragmentation tools measure CPCR fragmentation. Area of the large circles (CPCRs), and total area of the components within the large circles (fragmentation factors), do not change from left to right. (A) represents decreasing effective mesh size, such that the changing configuration of the disturbance components decreases the probability of animals meeting without having to cross a disturbance zone, (A,B, and C) represent increasing edge to area ratio, such that the changing configuration of the disturbance components increases edge habitat without changing disturbed area, and (A, B, and C) represent increasing fragmentation extent, such that the changing configuration of the disturbance components decreases the potential for caribou to distance themselves away from disturbances, while remaining within the CPCR.

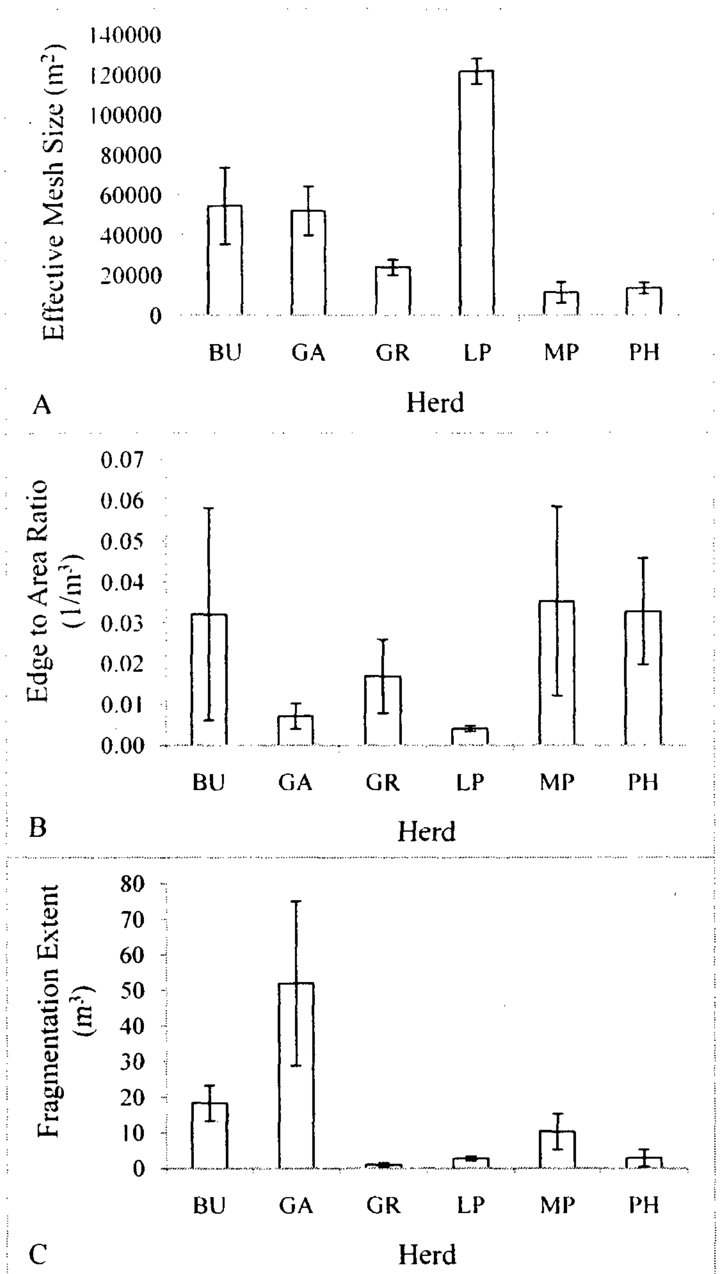

Figure 7: Difference between caribou herds in respect to average yearly (A) effective mesh size (a measure of area available before having to cross disturbance layer), (B) edge to area ratio (a measure of edge effects), and (C) fragmentation extent (a measure of whether disturbance layer is clumped or dispersed) from 2005-2008 in Newfoundland, Canada. Error bars are 1 SE of the mean. Abbreviations for herds: BU= Buchans, GA = Gaff Topsail, GR = Grey River, MP = Mount Peyton, LP = LaPoile, and PH = Pot Hill.

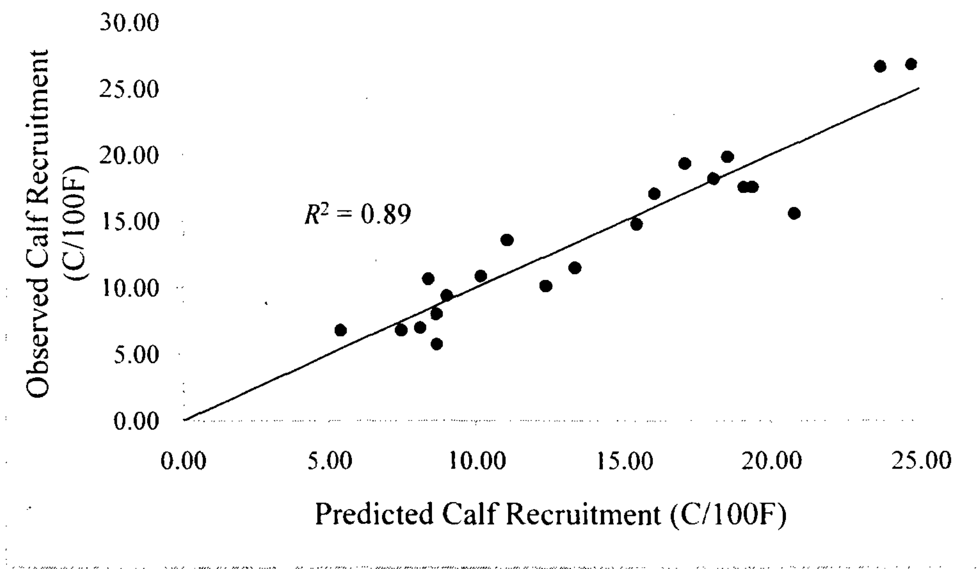

Figure 8: Observed calf recruitment (calves/100 females) from 2005-2008 in Newfoundland, Canada, versus calf recruitment (calves/100 females) as predicted by top AIC_c ranked linear mixed model (accounting for herd) with year as a random term; recruitment = herd + total disturbance + mixed forest + wetland + edge to area ratio. The line represents where the points would lie if the model fit the observed calf recruitment perfectly.

General Discussion

This study explored the possibility of using several measures of landscape structure to explain calf recruitment among declining populations of woodland caribou. Shifting from behavioural- habitat selection studies to those that quantify relationships between factors we can manage and caribou vital rates was suggested to aide in the transition from scientific research to management recommendations (Gill and Sutherland 2000, Gill et al. 2001, Wittmer et al. 2007). This was done by relating calf recruitment to measures of landscape structure. There were five objectives; the first three related to landscape composition and are covered in Chapter 1, while the last two related to landscape configuration and are covered in Chapter 2.

I found that calf recruitment was significantly related to total disturbance area, such that herd calf recruitment rate was expected to decrease by 1 with every additional $20km^2$ of total disturbance within female's CPCRs. Wittmer et al. (2007) and Sorensen et al. (2008) also found human disturbance to negatively influence female survival and population growth (respectively). I also found that mixed forest was the only landcover type that was significantly related to calf recruitment, the relationship also being negative. Wittmer et al. (2007) found similar trends with early seral forest stages and female caribou survival. The model that included only landscape composition parameters that best explained variation in calf recruitment included negative effects of total disturbance area and of deciduous forest area, and had a good predictive power (relationship between predicted and observed values: $R^2 = 0.81$). Landscape disturbance and the associated loss of coniferous forests and increase in early seral stage forests has been suggested to limit forage availability (Nelleman et al. 2000), increase caribou densities away from the disturbance source (Nellemann and Cameron 1996), increase apparent competition (Laliberte and Ripple 2004, Boisjoly et al. 2010), and increase predator efficiency (Edmonds and Bloomfield 1984), which can result in decreased reproductive rates (Weladji and Forbes 2002, Cameron et al. 2005), poorer predator avoidance abilities (Bergerud et al. 1990), and increased predation pressure (James and Stuart-Smith 2000).

Similar to Johnson et al. (2002) and Wittmer et al. (2007), I found that none of the three measures of landscape configuration in terms of disturbance-mediated fragmentation were significantly related to calf recruitment, and were hence of less importance than measures of overall habitat-loss. I found that the edge to area ratio fragmentation measure substantially improved all of the previously generated top ranked models, increasing the ability to predict calf recruitment from 0.81 to 0.89 (R^2 value of the top model). The effective mesh size and fragmentation extent fragmentation measures did not improve the previously generated models. An importance of accounting for fragmentation in determining the effects of disturbance on calf recruitment was expected, as it has been found to negatively affect caribou ecology in many other studies (James and Stuart-Smith 2000, Dyer et al. 2001, Cameron et al. 2005, Schindler et al. 2006, Weir et al. 2007).

Management Recommendations

This study shows that human disturbance sources and their impacts on landscape composition and configuration are influencing the decline of Newfoundland's woodland caribou. Understanding direct relationships between landscape factors that can be controlled and vital rates is of utmost importance in order to actively contribute to wildlife conservation. Such a shift in conservation related research would improve our ability to relate scientific research findings to wildlife management and land-use problems. This study suggests that woodland caribou calf recruitment may improve if the predation pressure mediated through landscape disturbance can be reduced. This could involve replanting clear-cut areas with coniferous seedlings to reduce regeneration time to climax forest communities. Additionally, any new human disturbance projects should be implemented in such a way that fragmentation is reduced, such as by logging one larger area as opposed to many smaller areas, or by restricting new power line development to already existing roadways. Given the long life span of woodland caribou and the lengthy process of forest conversion, followed by colonization by other ungulates and eventually their associated predators, I recommend that studies like this be done on long-term data sets so that the delayed effects of forest disturbance can be recognized (James et al. 2004).

References

Akaike. H. 1973. Information theory as an extension of the maximum likelihood principle. In: B. N. Petroy and F. Csaki (eds.) 2nd International Symposium on Information Theory, Akademia Kiado, Budapest, pp 267–281.

Allen, G. M. and T. Barbour. 1937. The Newfoundland wolf. Journal of Mammalogy 18:229-234.

Apps, C. and B. McLellan. 2006. Factors influencing the dispersion and fragmentation of endangered mountain caribou populations. Biological Conservation 130:84-97.

Bender, D. J., L. Tischendorf, and L. Fahrig. 2003. Using patch isolation metrics to predict animal movement in binary landscapes. Landscape Ecology 18:17-39.

Bergerud, A. T. 1971. The population dynamics of Newfoundland Caribou. Wildlife Monographs 25: 3-55.

_____. 1972. Food habits of Newfoundland caribou. Journal of Wildlife Management 36:913-923.

_____. 1992. Rareness as an antipredator strategy for moose and caribou. Pages 1008-1021 *in* D. R. McCullough, and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Science, London, United Kingdom.

_____. A. T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? Rangifer, Special Issue 9:95-116.

Bergerud, A. T., R. Ferguson, and H. E. Butler. 1990. Spring migration and dispersion of woodland caribou at calving. Animal Behaviour 39:360-368.

Boisjoly. D., J-P. Ouellet, and R. Courtois. 2010. Coyote habitat selection and management implications for the Gaspesie Caribou. Journal of Wildlife Management 74:3-11.

Bradshaw, C. J. A., S. Boutin, and D. M. Herbert. 1997. Effects of petroleum exploration on woodland caribou in northeastern Alberta. Journal of Wildlife Management 61:1127-1133.

Bradshaw, C. J. A., S. Boutin, and Herbert, D. M. 1998. Energetic implications of disturbance carused by petroleum exploration to woodland caribou. Canadian Journal of Zoology 76:1319-1324.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York, New York, USA.

Calbrese, J. M. and W. F. Fagan. 2004. A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and the Environment 2:529-536.

Cameron, R., W. Smith, R. White, and B. Griffith. 2005. Central Arctic Caribou and petroleum development: Distributional, nutritional, and reproductive implications. Arctic 58:1-9.

Canadian Association of Zoo and Wildlife Veterinarians. 2009. The chemical immobilization of wildlife- 3rd Edition. Canadian Association of Zoo and Wildlife Veterinarians.

Carleton, T. J. and P. MacLennan. 1994. Woody vegetation responses to fire versus clear-cut logging: A comparative survey in the central Canadian boreal forest. Ecoscience 1:141-152.

Chan-McLeod, A. C. A., R. G. White, and D. E. Russell. 1999. Comparative body composition strategies of breeding and non-breeding caribou. Canadian Journal of Zoology 77:1901-1907.

Channell, R. and M. V. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. Nature 403:84-86.

Chetkiewicz, C. L. B., C. C. S. Clair, and M. S. Boyce. 2006. Corridors for conservation: Integrating pattern and process. Annual Review of Ecology, Evolution, and Systematics 37:317-342.

Chubbs, T. E., L. B. Keith, S. P. Mahoney, and M. J. McGrath. 1993. Response of woodland caribou (*Rangifer tarandus caribou*) to clear-cutting in East-Central Newfoundland. Canadian Journal of Zoology 71:487-493.

COSEWIC. 2002. COSEWIC assessment and update status report on the woodland caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada.

Courtois, R., J. P. Ouellet, L. Breton, A. Gingras, and C. Dussault. 2007. Effects of forest disturbance on density, space use, and mortality of woodland caribou. Ecoscience 14:491-498.

Crete, M. and A. Desrosiers. 1995. Range expansion of coyotes, *Canis latrans*, threatens a remnant herd of caribou, *Rangifer tarandus*, in southeastern Quebec. Canadian Field-Naturalist 109:227-235.

Cumming, H. G., D. B. Beange, and G. Lavoie. 1996. Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk. Rangifer Special Issue 9:81-94.

Daaman, A. W. H. 1983. An ecological subdivision of the island of Newfoundland. Monographs in Biology 48:163-206.

Davidson, C. 1998. Issues in measuring landscape fragmentation. Wildlife Society Bulletin, 26:32-37.

Dumont, A. 1993. Impact des randonners sur les caribou *Rangifer tarandus caribou* du parc de la Gaspesie. MSc. Thesis. Universite Laval, Quebec, Canada.

Dunford, J. S., P. D. McLoughlin, F. Dalerum, and S. Boutin. 2006. Lichen abundance in the peatlands of northern Alberta: implications for boreal caribou. Ecoscience 13:469-474.

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

Edmonds, E. J. and M. Bloomfield. 1984. A study of woodland caribou (*Rangifer tarandus caribou*) in West Central Alberta, 1979-1983. Page 203 *in* Alberta Energy and Natural Resources, Fish and Wildlife Division, Edmonton, Alberta.

Eigenbrod, F., S. J. Hecnar, and L. Fahrig. 2008. Accessible habitat: an imporved measure of the effects of habitat loss and roads on wildlife populations. Landscape Ecology 23:159-168.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics 34:487-515.

Forbes, B., J. Ebersole, and B. Strandberg. 2001. Anthropogenic disturbance and patch dynamics in circumpolar arctic ecosystems. Conservation Biology 15:954-969.

Gill, J. A. and W. J. Sutherland. 2000. The role of behavioural decision-making in predicting the consequences of human disturbance. In: Gosling, L.M. and

Sutherland, W. J. (Eds.)., Behaviour and Conservation. Cambridge University Press, Cambridge.

Gill, J. A., K. Norris, and W. J. Sutherland. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation 97:265-268.

Girvetz, E. H. and S. E. Greco. 2007. How to define a patch: a spatial model for hierarchically delineating organism-specific habitat patches. Landscape Ecology 22:1131-1142.

Girvetz, E. H., J. H. Thorne, A. M. Berry, and J. A. G. Jaeger. 2008. Integration of landscape fragmentation analysis into regional planning: A statewide multi-scale case study from California, USA. Landscape and Urban Planning 86:205-218.

Gustine, D. D., K. L. Parker, R. J. Lay, M. P. Gillingham, and D. C. Heard. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. Wildlife Monographs. 165:1-32.

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

Hagemoen, R. I. and E. Reimers. 2002. Reindeer summer activity pattern in relation to weather and insect harassment. Journal of Animal Ecology 71:883-892.

Hansen, M.J., S. E. Franklin, C. J. Woudsma, and M. Peterson. 2001. Caribou habitat mapping and fragmentation analysis using Landsat MSS, TM, and GIS data in the North Columbia Mountains, British Columbia, Canada. Remote Sensing of Environment 7:50-65.

Harrington, F. H. 2001. Caribou, military jets and noise: the interplay of behavioural ecology and evolutionary psychology. Rangifer. Special Issue 14:73-80.

Helle, T. and I. Kojola. 1994. Body mass variation in semi domestic reindeer. Canadian Journal of Zoology 72:681-688.

Hins, C., J. Ouellet, C. Dussault, and M. St-Laurent. 2009. Habitat selection by forest-dwelling caribou in managed boreal forest of eastern Canada: Evidence of a landscape configuration effect. Forest Ecology and Management 257:636-643.

Jaeger, J. A. G. 2000. Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Landscape Ecology 15:115-130.

Jaeger, J. A. G., J. Bowman, J. Brennan, L. Fahrig, D. Bert, J. Bouchard, N. Charbonneau, K. Frank, B. Gruber, and K. T. von Toschanowitz. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecological Modelling 185:329-348.

Jaeger, J. A. G., H-G. Schwarz-von Raumer, H. Esswein, M. Muller, and M. Schmidt-Luttmann. 2007. Time series of landscape fragmentation caused by transportation infrastructure and urban development: a case study from Baden-Wurttemberg (Germany). Ecology and Society 12:22-50.

Jalkotzy, M. G., P. I. Ross, and M. D., Nasserden. 1997. The effects of linear developments on wildlife: a review of selected scientific literature. Arc Wildlife Services, Calgary, Alberta, Canada.

James, A., S. Boutin, D. Hebert, and A. Rippin. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. Journal of Wildlife Management 68:799-809.

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

Johnson, C. and M. Gillingham. 2008. Sensitivity of species-distribution models to error, bias, and model design: An application to resource selection functions for woodland caribou. Ecological Modelling 213:143-155.

Johnson, C. J., K. L. Parker, D. C. Douglas, C. Heard, and M. P. Gillingham. 2002. A multiscale behavioural approach to understanding the movements of woodland caribou. Ecological Applications 12:1840-1860.

Johnson, C., M. S. Boyce, R. Mulders, A. Gunn, R. J. Gau, H. D. Cluff, and R. L. Case. 2004. Quantifying patch distribution at multiple spatial scales: applications to wildlife-habitat models. Landscape Ecology 19:869-882.

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

Kindlmann, P. and F. Burel. 2008. Connectivity measures: a review. Landscape Ecology 23:879-890.

Kinley, T. A. and C. D. Apps. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. Wildlife Society Bulletin 29:158-164.

Laliberte, A. S. and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. Bioscience 54:123-138.

Leu, M., S. E. Hanser, and S. T. Knick. 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. Ecological Applications 18:1119-1139.

Lindenmayer, D. B. and J. F. Franklin. 2002. Conserving Forest Biodiversity: A Comprehensive Multiscales Approach. Island Press, Washington.

Mahoney. S. P. and J. A. Schaefer. 2002a. Long-term changes in demography and migration of Newfoundland caribou. Journal of Mammalogy 83:957-963.

Mahoney, S. P. and J. A. Schaefer. 2002b. Hydroelectric development and the disruption of migration in caribou. Biological Conservation 107:147-153.

Mahoney, S. P. and J. Virgl. 2003. Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland. Canadian Journal of Zoology 81:321-334.

Mahoney, S. P., F. Norman, T. Porter, J. N. Weir, and J. G. Luther. 2008. Influence of juvenile survival on population trends of insular Newfoundland caribou. Page 7, poster *in* 12th North American Caribou Workshop, Nov 3-6, 2008. Goose Bay, Canada.

McLaren, B. E., B. A. Roberts, N. Djan-Chekar, and K. P. Lewis. 2004. Effects of overabundant moose on the Newfoundland landscape. Alces 40:45-60.

McLoughlin, P. D., J-M. Gaillard, M. S. Boyce, C. Bonenfant, F. Messier, P. Duncan, D. Delorme, B. Van Moorter, S. Said, and F. Klein. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. Ecology 88:3192-3201.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. Pages 223-249 *in* The American Midland Naturalist Journal.

Mosnier, A., J. P. Ouellet, and R. Courtois. 2008. Black bear adaptation to the low productivity in the boreal forest. Ecoscience 15:485-497.

Natural Resources Canada. 2009. The State of Canada's Forests. *in* Annual Report 2009. Available from: canadaforests.nrcan.gc.ca. Accessed 5 Jan 2009.

Nellemann, C. and R. D. Cameron. 1996. Effects of petroleum development on terrain preferences of calving caribou. Arctic 49:23-28.

Nellemann, C., P. Jordhoy, O. Stoen, and O. Strand. 2000. Cumulative impacts of tourist resorts on wild reindeer (*Rangifer tarandus tarandus*) during winter. Arctic 53:9-17.

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

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

Oehler, J. D. and J. A. Litvaitis. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. Canadian Journal of Zoology 74:2070-2079.

Quinn, G. P. and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, New York, New York, USA.

Rettie, W. and F. Messier. 1998. Dynamics of woodland caribou populations at the souther limit of their range in Saskatchewan. Canadian Journal of Zoology 76:251-259.

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

Rheault, H., P. Drapeau, Y. Bergeron, and P-A. Esseen. 2003 Edge effects on epiphytic lichens in managed black spruce forests of eastern North America. Canadian Journal of Forest Research 33:23-32.

Rodgers, A. R., A. P. Carr, H. L. Beyer, L. Smith, and J. G. Kie. 2007. HRT: Home Range Tools for ArcGIS. Ontario Ministry of Natural resources, Center for Northern Forest Ecosystem Research, Thunder Bay, Ontario.

Schaefer, J. and S. Mahoney. 2007. Effects of progressive clearcut logging on Newfoundland Caribou. Journal of Wildlife Management 71:1753-1757.

Schindler, D. W., D. Walker, T. Davis, and R. Westwood. 2006. Determining effects on an all weather logging road on winter woodland caribou habitat use in south-eastern Manitoba. Rangifer, Special Issue 17:209-217.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern Bristish Columbia. Canadian Journal of Zoology 70:46-52.

Simpson, K. and E. Terry. 2003. Impacts of backcountry recreation activities on mountain caribou. Wildlife Working Report No. WR-99, Ministry of Environment, Lands and Parks, Victoria, BC.

Smith, K., E. Ficht, D. Hobson, T. Sorensen, and D. Hervieux. 2000. Winter distribution of woodland caribou in relation to clear-cut logging in west-central Alberta. Canadian Journal of Zoology 78:1433-1440.

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

St-Laurent, M-H., C. Dussault, J. Ferron, and R. Gagnon. 2009. Dissecting habitat loss and fragmentation effects following logging in boreal forest: Conservation perspectives from landscape simulations. Biological Conservation 142:2240-2249.

Stephens, P. A., S. W. Buskirk, G. D. Hayward, and C. M. Del Rio. 2005. Information theory and hypothesis testing: a call for pluralism. Journal of Animal Ecology 42:4-12

Stuart-Smith, A. K., C. J. A. Bradshaw, S. Boutin, D. M. Hebert, and A. B. Rippin. 1997. Woodland Caribou relative to landscape patterns in Northeastern Alberta. Journal of Wildlife Management 61:622-633.

Theobald, D. M., J. R. Miller, and N. Thompson Hobbs. 1997. Estimating the cumulative effects of development on wildlife habitat. Landsacpe and Urban Planning 39:25-36.

Thomas, D. C. 1982. The relationship between fertility and fat reserves of Peary Caribou. Canadian Journal of Zoology 60:597-602.

Turner, M. G., R. H. Gardner, and R. V. Oneill. 2001. Landscape ecology in theory and practice. Springer-Verlag, New York, NY.

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

Vistnes, I., C. Nellemann, P. Jordhoy, and O. Strand. 2001. Wild reindeer: impacts of progressive infrastructure development on distribution and range use. Polar Biology 24:531-537.

Vors, L., J. Schaefer, B. Pond, A. Rodgers. and B. Patterson. 2007. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. Journal of Wildlife Management 71:1249-1256.

Weir, J., S. Mahoney, B. McLaren, and S. Ferguson. 2007. Effects of mine development on woodland caribou Rangifer tarandus distribution. Wildlife Biology 13:66-74.

Weladji, R. B. and B. C. Forbes. 2002. Disturbance effects of human activities on *Rangifer tarandus* habitat: implications for life history and population dynamics. Polar Geography 26:171-186.

Weladji, R. B., O. Holand, and T. Almoy. 2003. Use of climatic data to assess the effect of insect harassment on the autumn weight of reindeer (*Rangifer tarandus*) calves. Journal of Zoology 260:79-85.

Wittmer, H. U., A. R. E. Sinclair, and B. N. McLellan. 2005a. The role of predation in the decline and extripation of woodland caribou. Oecologia 144:257-267.

Wittmer, H., B. McLellan, D. Seip, J. Young, T. Kinley, G. Watts, and D. Hamilton. 2005b. Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia, Canada. Canadian Journal of Zoology 83:407-418.

Wittmer, H., B. McLellan, R. Serrouya, and C. Apps. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. Journal of Animal Ecology 76:568-579.

Wulder, M., J. White, S. Magnussen, and S. McDonald. 2007. Validation of a large area land cover product using prupose-acquired airborne video. Remote Sensing of Environment 106:480-491.

Zollner, P. A. and S. L. Lima. 1999. Illumination and the perception of remote habitat patches by white-footed mice. Animal Behaviour 58:489-500.