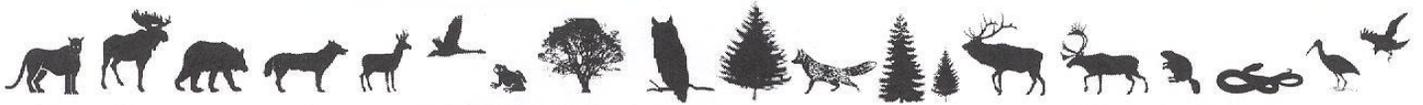

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Original Research

Effects of Snowmachine Disturbance on the Energetics and Habitat Selection of Caribou (*Rangifer tarandus*) in Gros Morne National Park, Newfoundland

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Abstract

Caribou (*Rangifer tarandus*) and other northern ungulates are increasingly exposed to snowmachine activity, but the implications of such exposure for energetics and habitat use are not fully understood. We assessed the influence of snowmachine exposure on the energy balance and habitat selection of caribou in Gros Morne National Park, Newfoundland, Canada. We assessed habitat selection of radio-collared females at 2 spatial scales, within the population range and the home range. Based on field observations of caribou reactions to provocation by snowmachine, we modelled the energetic costs of disturbance as 1 event and extrapolated its effects on body mass during winter. During winter, females exhibited apparent preference for snowmachine trails at the scale of the population range, but neither preference nor avoidance at the scale of the home range. This broad-scale pattern likely reflects the spatial association of trails with lowlands and the more favourable nival conditions there. The energetic cost of 1 snowmachine encounter was negligible; we surmise it would require far more encounters than are likely to produce a significant and harmful loss in body mass. We conclude that the lack of response to snowmachines may represent habituation, a lack of snowmachine-free alternative habitat, and/or risk-prone foraging by this population.

Key Words: Caribou, Disturbance, Energetics, Habitat Selection, Snowmobile.

INTRODUCTION

Industrial and recreational activity can have serious effects on wildlife, including displacing ungulates from habitat (Cameron 1983; Nellemann and Cameron 1998; Nellemann *et al.* 2000; Vistnes and Nellemann 2001; Harris *et al.* 2014) and heightening energy expenditures (Shank 1979; Shideler *et al.* 1986; Tyler 1991; Bradshaw *et al.* 1998; Olliff *et al.* 1999). For northern ungulates, such as caribou (*Rangifer tarandus*), disturbance may be especially significant in winter when snowcover imposes added energetic costs of locomotion (Fancy and White 1987) and foraging (Fancy and White 1985), and when avoidance may run counter to the seasonal adaptations of reduced activity, food intake, and metabolic rate (Moen *et al.* 1982; Hudson and Christopherson 1985). Recurring disturbance can have a profound negative effect on the body weights of wild reindeer (*R. t. tarandus*) by altering activity budgets (Hagemoen and Reimers 2002) and grazing intensity (Colman *et al.* 2003).

Snowmachine disturbance of wildlife has been a concern since the rising popularity of snowmobiles in the 1960s (Eckstein *et al.* 1979; Freddy *et al.* 1986; Dustin and Schneider 2005). Experimental studies with caribou have shown that snowmobiles provoke flight responses (Tyler 1991; Mahoney *et al.* 2001; Reimers *et al.* 2003; Powell 2004) that have a small but measurable energetic cost (Tyler 1991; Reimers *et al.* 2003; Powell 2004; but see Bradshaw *et al.* 1998). Snowmachines can displace caribou from habitat (Seip *et al.* 2007) and can invoke avoidance responses that may interfere with normal feeding and resting (Mahoney *et al.* 2001). Although low levels of disturbance are unlikely to affect the fitness of individual caribou, repeated and frequent disturbance may negatively influence caribou during the

time of year when extra energy expenditure can be most harmful (Adamczewski *et al.* 1993). To date, however, energy loss and habitat displacement have not been considered together, even though this approach could produce more robust understanding (Reimers and Colman 2003).

A particular obstacle has been difficulty in knowing the location of snowmobile activity coinciding with observations of caribou. Most studies have been restricted in time and space – for example, to a few areas or linear features such as frozen rivers (Tyler 1991), to a high-use area (Seip *et al.* 2007), or to short duration (Reimers *et al.* 2003). Gros Morne National Park (GMNP) presents an uncommon opportunity because snowmachine trails are mapped. Local residents use these trails for access to timber along the coastal lowlands; they can travel throughout the whole trail system in the Park if snow conditions permit. Therefore, caribou space-use can be measured as the known proximity to these trails.

Following a companion behavioural study (Mahoney *et al.* 2001), we assessed the effect of snowmobiles on the habitat use and energetics of caribou in GMNP. To quantify habitat selection, we analyzed satellite and GPS telemetry data of adult female caribou using Euclidean distances (Conner *et al.* 2003); this approach readily handles responses to linear features (Conner and Plowman 2001) and is especially suited to studies of *Rangifer* whose avoidance reactions may extend kilometres from anthropogenic features (Mahoney and Schaefer 2002; Vistnes and Nellemann 2008). To estimate the cost to individual caribou, we applied an energetics model (Bradshaw *et al.* 1998) to direct behavioural observations of caribou experimentally disturbed by snowmobiles (Mahoney *et al.* 2001). We used this model to

estimate the number of snowmachine disturbance events required to cause mass loss sufficient to affect caribou survival and productivity. We used these multiple lines of evidence – behaviour, energetics, and habitat selection at multiple scales – to increase our understanding of the potential implications for caribou.

STUDY AREA

Gros Morne National Park (1,945 km²) is situated on the western coast of Newfoundland (49°34'N, 57°45'W; Figure 1). The Park comprises 2 distinct physiographic regions. The broad coastal lowlands of the western half are composed of extensive bogs and dispersed coniferous forest of primarily balsam fir (*Abies balsamea*) and black spruce (*Picea mariana*), and smaller patches of white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*). The lowlands are wind-swept; snow is not deep and snow crusting is minimal; such conditions provide easier access to forage (Fancy and White 1985). The upland region, a portion of the Long Range Mountains, runs north-south through the central region of the Park, rising abruptly on the western edge of the lowlands and sloping more gradually on the Park's eastern front. The upland vegetation is composed primarily of heath with trees in krummholz form. Winters are long and snow cover is typically continuous from December through April.

Snowmachine activity occurs primarily from February to April, depending on snow conditions. For residents of GMNP, snowmachine travel is permitted in most of the Park. However, snowmachine traffic in the lowlands is naturally confined by snow conditions to specific trails; those most heavily used traverse the communities along the Park's western perimeter, providing residents with access to timber harvesting (Figure 1). In the uplands at the time of this study, residents and non-residents could travel freely but tended to stay along easily traveled routes, such as wetlands and valleys. Although we use the term 'trails' for consistency, these trails were often broad travel routes or corridors (<500 m wide), especially in the uplands, rather than narrow linear features. Snowmachine traffic in the uplands was primarily recreational during weekends (S. Taylor, personal observations; Taylor and Simpson 2005).

Snowmachine trails were mapped at the time of the study using a combination of GPS, topographic maps, and 1:12,500 aerial photographs, as well as reports from knowledgeable park residents and snowmachine users. To quantify use, electronic trail counters (Models 1300, 600 and 900; Interprovincial Travel Services) were deployed along the main access points of the 5 primary park trails (Figure 1), January-April, 1993-1995. Counters were checked for

sensitivity and accuracy, and batteries were changed at regular intervals (Reid 1993, 1994). The sensitivity of counters was calibrated so that only large objects on the trail would be tallied; sensitivity was repeatedly tested in trials and checked during the study. Average use of individual trails was variable, ranging from 2-41 vehicle passes per day (Table 1).

Gros Morne caribou are migratory, moving from the lowlands in the winter to uplands in the summer. This population increased in synchrony with the other herds in the Newfoundland island population – i.e., from an estimated 1870 animals in 1994 to 2877 animals in 1997 (Bastille-Rousseau *et al.* 2013). During winter, most caribou utilized the lowlands near the coast; a small number (ca. 150 animals) were regularly observed in the uplands (S. Gerrow, 2016, GMNP, personal communication).

METHODS

Habitat selection

Data collection

Twenty-one adult female caribou were live-captured in January 1993 and 1996, and fitted with 10 Argos platform transmitter terminals (PTTs) and 11 global positioning system (GPS) transmitters (Lotek Wireless Inc.; Service Argos). PTTs were programmed to transmit every 2 d, GPS collars to collect locations every 3 h. Animals were weighed and live-captured and handled in accordance with the guidelines from the American Society of Mammalogists (Sikes *et al.* 2011).

Corresponding to periods of high snowmachine use, we included locations from February 1 to April 30 in all years. Before analysis, we removed erroneous data. For PTTs, we used the best quality class, and for GPS, we excluded 2-dimensional fixes with a dilution of precision greater than 5. The portion of the data discarded represented roughly three-quarters of the PTT data, and 7.4% of the GPS data. These 2 platforms differed substantially in accuracy (for PTTs, ≥ 100 m; for GPS, often <50 m). Such discrepancies can be serious for resource selection functions (Morehouse and Boyce 2013). However, the distance-based approach – based on animals' proximity rather than occupancy of habitat patches – is less sensitive to telemetry error (Conner and Plowman 2001). For analysis, we retained animals ($n = 20$) with at least 7 locations after filtering.

The study area was bounded by ≤ 10 km from snowmachine trails, excluding south of Bonne Bay (Figure 1) where no collared caribou were found. This distance represents the approximate maximum extent of avoidance, based on caribou studies in Newfoundland (Mahoney and Schaefer 2002; Schaefer and Mahoney 2007; Weir *et al.*

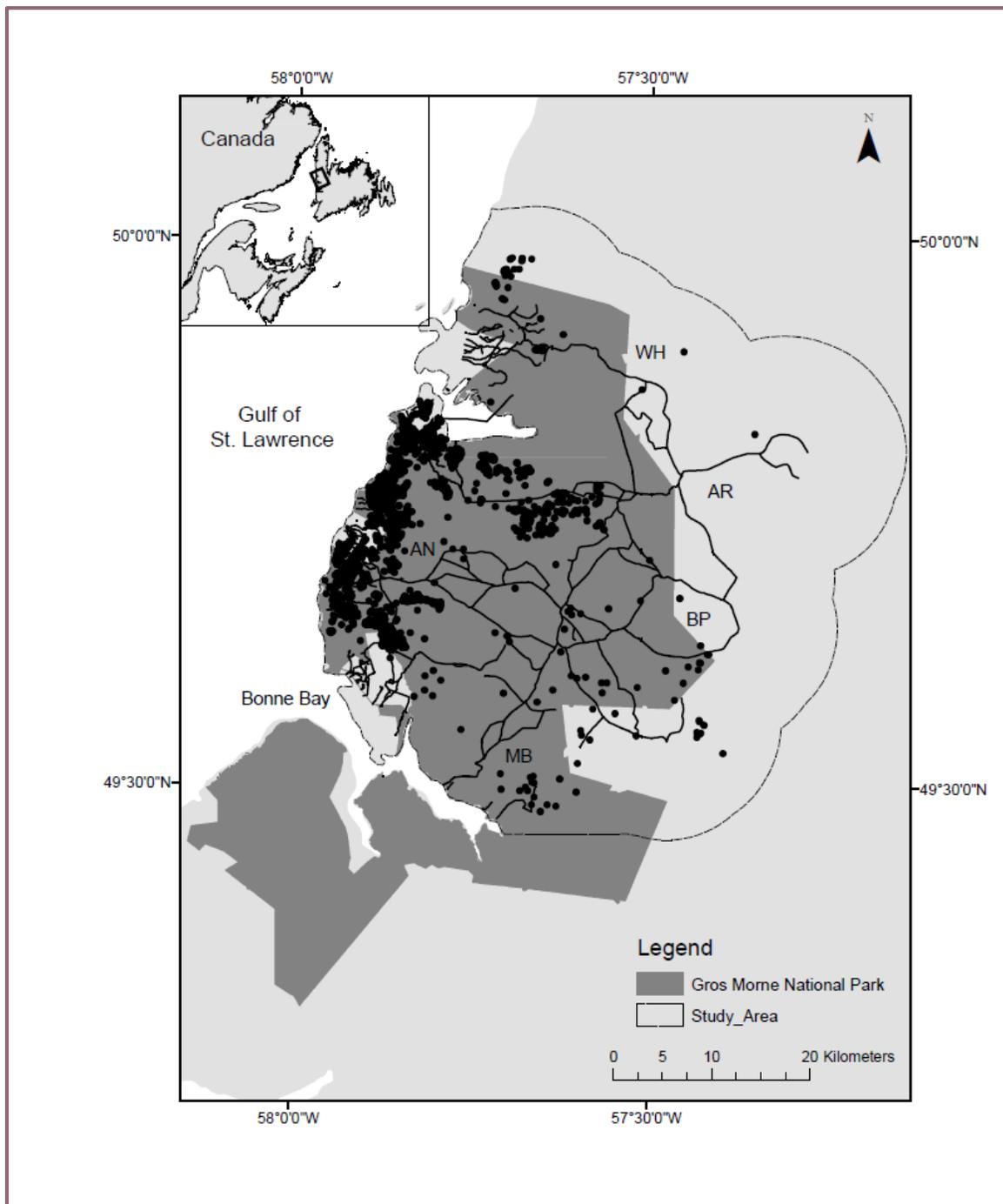


Figure 1. Locations of snowmachine trails (black lines) and the study area based on caribou locations (black dots; 1993-1998) in Gros Morne National Park (GMNP), Newfoundland. Trails are labelled as WH (Western Hills), AR (Arm Pond), BP (Beaver Pond), MB (Mills Brook), and AN (Angle Pond). Communities in GMNP are the colour of the background. The dashed line represents 10 km from the snowmachine trails and the effective study area.

Table 1. Frequency of snowmachine use and the mean number of snowmachines per day along five main trails, Gros Morne National Park, Newfoundland, January-April, 1993-1995.

Trail	1993			1994			1995		
	Total number	Days	Mean	Total number	Days	Mean	Total number	Days	Mean
	of snowmachines		number per day	of snowmachines		number per day	of snowmachines		number per day
Angle Pond	1168	105	11.1	136	55	2.5	837	56	14.9
Arm Pond	869	41	21.2	409	69	5.9	452	107	4.2
Beaver Pond	352	33	10.7	629	85	7.4	641	107	6.0
Mill Brook	702	109	6.4	366	67	5.5	1954	48	40.7
Western Hills	985	80	12.3	240	48	5.0	1542	105	14.7

2007), British Columbia, and Canadian Arctic (e.g., Polfus *et al.* 2011; Boulanger *et al.* 2012).

Habitat composition and habitat selection

To identify the habitat types, we used a supervised ecological landcover classification (ELC) developed for caribou in Newfoundland (Integrated Informatics 2013). The raster-based ELC consisted of remotely sensed data at 30-m resolution (Landsat Thematic Mapper [TM] and Enhanced Thematic Mapper [ETM+]; Wulder *et al.* 2008) comprising 10 habitat types with an accuracy of 76.4% (Table 2), overlaid with the network of trails (Figure 1). We treated trails as linear elements and included distance to the coast of the Gulf of St. Lawrence (“Coast”) to account for the apparent preference of caribou for lowlands.

Habitat selection was quantified using Euclidian distance-based analysis (ED; Conner and Plowman 2001; Conner *et al.* 2003). This approach entails comparing distances, from animal locations versus random locations, to the nearest representative of each habitat class (Table 2). We therefore computed distances of 2 kinds: (A) from animal locations to the nearest parcel or segment of each habitat type or linear feature; and (B) from locations generated by a uniform random distribution to the nearest parcel or segment of each habitat type or linear feature (Conner *et al.* 2003; Schaefer and Mahoney 2007). We conducted the analysis at 2 spatial scales: within the population range (2nd order) and within the home range (3rd order; Johnson 1980). For the 2nd order, availability was set as random points within the study area (≤ 10 km from radio-locations; Figure 1); for the 3rd order, it was set as random points within 95% minimum convex polygons (MCPs) for each caribou each year. We denoted

‘use’ as random locations within the MCP home range for each caribou each year for the 2nd order analysis, and as radio-locations for 3rd order analysis. Such a nested hierarchy – where use at one level is recast as availability at a finer level – can strengthen inferences about habitat selection (Schaefer and Messier 1995; Mayor *et al.* 2009).

We calculated the distance of each radiolocation to the nearest representative of each of the 12 habitat types, including snowmachine trails and the coast. We repeated this procedure for 5,000 randomly distributed points within the study area, i.e., sufficient to stabilize the average distances to each habitat type (Obbard *et al.* 2010). We treated the animal as the experimental unit ($n = 20$) by computing average distances for each individual per year. Preference was inferred where animal distances were closer than expected (based on availability); avoidance was inferred where animal distances were further than expected (Conner *et al.* 2003).

We computed a vector of log-ratios ($d = \log [\text{use}/\text{availability}]$) for each habitat type. In general, these ratios of use to availability were not normally distributed and were log-transformed to meet the assumption of normality. To test for avoidance and preference of each habitat type, we used one-sample *t*-tests against the null hypothesis that each $d \approx 0$ (Conner and Plowman 2001). Despite the multiple tests, we set $\alpha = 0.05$ to balance the risks of type I and type II errors. We conducted analyses using ArcGIS 10.1 (ESRI 2014) and program R (R Core Team 2013).

An important feature of ED is its sensitivity to the arrangement of habitats on the landscape. Apparent selection for 1 habitat type may result from its proximity to

Table 2. Ecological land cover classification scheme for the study area, Gros Morne National Park, Newfoundland, and other variables used in the Euclidian distance-based analysis.

Habitat type	Description
Broadleaf forest	Dominated by broadleaf trees, namely white birch with a tree canopy of greater than 25% coverage.
Conifer forest	Dominated by balsam fir or black spruce but with some larch; the shrub layer dominated by ericaceous species.
Conifer scrub	Plant species similar to the conifer forest but with poor growing conditions producing a stunted tree layer and various ericaceous shrubs; often found in the transition zone between conifer forest and lichen heathland.
Mixedwood forest	Species-rich and may be transitional between conifer forest and broadleaf forest; contains black spruce, balsam fir, and white birch, with a shrub layer similar to that found in conifer forest.
Rocky barren	Windswept and dominated by bedrock, exposed soil, stone, and boulders; the shrub layer is composed mainly of ericaceous shrubs; ground cover consists of grasses, lichens, mosses, and smaller berry plants such as black crowberry.
Wetland	Composed predominantly of fens, bogs, and saturated soil; open water may be present; tree layer is sparse to none; shrubs are sparse and dominated by ericaceous shrubs; the ground layer is composed of sphagnum moss, deergrass, and sedges.
Water	Lakes, reservoirs, rivers, and salt water.
Lichen heathland	A non-forested shrub-dominated habitat found on hummocky terrain and may have thin soils with exposed bedrock; ericaceous shrubs are the dominant plant type; tree species are typically stunted; the ground layer is often dominated by ground lichens.
Exposed earth or anthropogenic	Non-vegetated habitat area characterized by river sediments, exposed soil, beaches, landings, mudflats, cutbacks, moraines, or other non-vegetated surfaces; anthropogenic areas: clearings for human settlements, major transportation routes, or other areas associated with anthropogenic impact.
Cut-block	Logged area generally in transition back to a forested state; site conditions are highly variable from wet to dry and from exposed to sheltered; the vegetation is also often highly variable, sometimes dominated by shrubs and at other times by herbs and grass species.
Coast	Distance to coast of Gulf of St. Lawrence.

another, truly preferred type (Bingham *et al.* 2010). In order to describe these spatial associations, we conducted Principal Components Analysis (PCA) from the distances to each habitat type from the random points (Zuur *et al.* 2007). We conducted these analyses using package *vegan* (Oksanen *et al.* 2013) in program R.

Energetic cost of snowmachine disturbance

One-disturbance event

Following Bradshaw *et al.* (1998), we calculated the energetic cost (COST) of a caribou's response to one-disturbance event as the sum of the metabolic costs of: (1) walking (per unit distance in moderate snow conditions) times the distance moved; (2) time spent in rapid locomotion; and (3) metabolic elevation due to excitement which can occur in the absence of overt behavioural reactions (MacArthur *et al.* 1979). From our companion study (Mahoney *et al.* 2001), we estimated the distance and

duration of these responses: the mean total distance walking (0.077 km for adults) and the mean total time in rapid avoidance movement (0.012 h). Prolonged excitement can increase metabolic costs by 10-25% of FMR (Geist 1978; Bradshaw *et al.* 1998), but disturbance times of caribou were short (< 3 min; Mahoney *et al.* 2001) and ungulate heart rates tend to return to normal 1-3 min after a disturbance (references in Reimers *et al.* 2003, p. 752). We estimated the duration of elevated metabolism from prolonged excitement at 6 min.

The energetic values used for walking in snow was 0.00264 MJ.kg⁻¹.km⁻¹ for adults (Boertje 1985), and the cost of running 0.0350 MJ.kg⁻¹.h⁻¹ for adults (Boertje 1985). We used a fasting metabolic rate (FMR) for adult barren-ground caribou of 0.403 MJ/kg^{0.75} (McEwan 1970; Fancy 1986) and added 10 to 25% of the FMR as the cost of prolonged

excitement due to disturbance (Geist 1978; Bradshaw *et al.* 1998).

We estimated adult and yearling body weights from caribou live-captured in GMNP, 1993-1997 (Mawhinney *et al.* 1998): adult male, 211.4 kg; adult female, 109.2 kg; yearling male, 116.0 kg; and yearling female, 85.5 kg.

In addition, because we received occasional but consistent reports of caribou deliberately pursued by snowmachines elsewhere in Newfoundland, we estimated more severe costs of disturbance. Lacking direct observation, we used values from Bradshaw *et al.* (1998) – i.e., 15 min of trotting and galloping and an additional 2.11 km of walking. Moreover, the energetic cost of locomotion increases exponentially with sinking depth in snow (Fancy and White 1987) with an inflection point of ca. 60% of the brisket height. To simulate deep snow in Newfoundland, we modified the values of snowmachine harassment using the mid-point between the inflection point and 100% of brisket height, i.e., 80% of brisket height.

Estimation of disturbance frequency for demographic effects

Typically, adult caribou lose 10-15% of their autumn mass during winter (Steen 1968; Dauphine 1976). To exceed the normal 15% mass loss maximum, caribou must lose, on average, an additional 2.5% of their autumn mass (LOSS; Bradshaw *et al.* 1998). In addition, we surmised that >20% mass loss resulted in death by starvation for adult males (an additional 5-10% loss of autumn mass) and in reduced calf production for adult females (Thomas *et al.* 1976; Adamczewski *et al.* 1987; Cameron and Ver Hoef 1994). We calculated the energy loss equivalences (ELOS; Bradshaw *et al.* 1998) for these additional mass loss thresholds (>15% and >20% for adults) by assuming a 90:10 ratio of fat to protein catabolism, using 39.3 MJ/kg and 5.0 MJ/kg as the respective energy-tissue conversions (Boertje 1985; Hudson and White 1985). These energy losses were divided by the cost of one disturbance event to determine the number of disturbances required to induce the prescribed changes in caribou mass (EVNT). In addition, we calculated COST as the percentage of the total daily energy expenditure (Fancy and White 1985; Reimers *et al.* 2003).

RESULTS

Habitat selection

During February - April, at the 2nd order of selection (within the population range), females were found closer than expected to the Coast and Snowmachine Trails (Figure 1), as well as to Broadleaf Forest and Wetlands (Table 3), further than expected from Conifer Scrub and young Cut Blocks (<5 years old; Table 3). At the 3rd order (within home ranges), patterns were less stark. Caribou were found closer

than expected only to Conifer Forest, Conifer Scrub, and Lichen/Heathland (Table 3).

The first 2 axes of PCA captured 46% of the variation (Figure 2). Snowmachine Trails were positively associated with the Coast and, to a lesser degree, Rocky Barrens, and negatively associated with Exposed Earth/Anthropogenic and Cut Blocks. Other habitats that tended to cluster together on the landscape were Lichen/Heathland, Conifer Forest and Conifer Scrub (Figure 2).

Energetic costs

Our model indicated the cost of 1 snowmachine encounter ranged from 0.07-0.16 MJ for adults and 0.06-0.09 MJ for yearlings; the percent of daily energy expenditure ranged from 0.22-0.30% (Table 4). We estimated it would take an enormous number of snowmachine events to produce mass loss sufficient to affect caribou survival or reproduction (Table 4). Based on our model, for yearling and adult caribou, ca. 1,000 and 2,000 encounters have the potential to cause 15% and 20% mass loss, respectively (Table 4). However, when caribou were deliberately harassed by snowmachine, the number of events required to cause the threshold mass loss fell to 122-248 events, and to 31-64 events when the snow sinking depth was high.

DISCUSSION

This study adds to the growing literature on the influence of snowmachines on caribou (Tyler 1991; Reimers *et al.* 2003; Powell 2004; Seip *et al.* 2007). In tandem with Mahoney *et al.* (2001), it is the first to examine a suite of consequences for behaviour, energetics, and habitat selection at multiple scales. These lines of evidence generally agreed. Low intensity disturbance (i.e., a slow but direct approach that ceases after the animals flee; Mahoney *et al.* 2001) appears to translate into minimal effects on caribou energetics. Female caribou often used, apparently even preferred, areas in close proximity to trails (Table 3). We acknowledge, nevertheless, that deducing the demographic consequences of energetic and behavioural responses must be done cautiously (Gill *et al.* 2001).

Habitat selection, in particular, occurs in a multivariate, multi-scaled setting. Although selection at broader scales may reveal the most salient limiting factors (Rettie and Messier 2000), snowmobile trails and other human features are not arranged at random on the landscape (Figure 2). Snow cover, in particular, can have profound influences on caribou distribution (Pruitt 1959). During winter, female caribou in GMNP avoided uplands, likely owing to the icy, wind-hardened upland snow (S. Mahoney, personal observations) and its attendant energetic costs for foraging (Fancy and White 1985). Snowmobile trails in our study area

Table 3. Winter habitat selection of female caribou based on the mean log ratios ($d \pm SE$) of use to availability, Gros Morne National Park, 1993-1998. Results are presented at the 2nd order (within population range) and 3rd order (within home range). Significant preference ($d < 0$) is noted in bold, significant avoidance ($d > 0$) is underlined.

Scale	Habitat	Mean \pm SE	t-value	df	p-value
Within population range	Exposed Earth/Anthropogenic (ANTH)	-0.015 \pm 0.053	-0.276	19	0.785
	Broadleaf Forest (BRFO)	-0.252 \pm 0.062	-4.045	19	0.001
	Coast (COAST)	-0.465 \pm 0.065	-7.202	19	<0.001
	<u>Conifer Forest (COFO)</u>	<u>0.167 \pm 0.049</u>	<u>3.368</u>	<u>19</u>	<u>0.003</u>
	Conifer Scrub (COSC)	0.014 \pm 0.065	0.222	19	0.827
	<u>Cut-block (<5 years) (CUT)*</u>	<u>0.317 \pm 0.02</u>	<u>15.983</u>	<u>9</u>	<u><0.001</u>
	Lichen/Heathland (LIHE)	-0.013 \pm 0.057	-0.226	19	0.823
	Mixedwood Forest (MIFO)	0.029 \pm 0.057	0.518	19	0.610
	Rocky Barren (ROBA)	-0.029 \pm 0.05	-0.58	19	0.569
	Snowmachine Trails (SMTR)	-0.477 \pm 0.071	-6.742	19	<0.001
	Water (WATER)	0.006 \pm 0.043	0.142	19	0.889
Wetland (WETL)	-0.174 \pm 0.052	-3.337	19	0.003	
Within home range	Exposed Earth/Anthropogenic (ANTH)	-0.042 \pm 0.038	-1.086	19	0.291
	Broadleaf Forest (BRFO)	-0.093 \pm 0.046	-2.024	19	0.057
	Coast (COAST)	-0.046 \pm 0.032	-1.416	19	0.173
	Conifer Forest (COFO)	-0.137 \pm 0.050	-2.710	19	0.014
	Conifer Scrub (COSC)	-0.157 \pm 0.062	-2.542	19	0.020
	Cut-block (<5 years) (CUT)*	-0.009 \pm 0.030	-0.299	9	0.772
	Lichen/Heathland (LIHE)	-0.158 \pm 0.045	-3.526	19	0.002
	Mixedwood Forest (MIFO)	-0.087 \pm 0.046	-1.906	19	0.072
	Rocky Barren (ROBA)	-0.002 \pm 0.029	-0.074	19	0.942
	Snowmachine Trails (SMTR)	-0.011 \pm 0.034	-0.305	19	0.763
	Water (WATER)	0.029 \pm 0.038	0.547	19	0.591
Wetland (WETL)	-0.212 \pm 0.105	-2.024	19	0.057	

* Not all animals were exposed to cut-blocks (<5-year-old-stands), resulting in fewer df.

were positively associated with coastal lowlands (Figures 1 and 2), which likely represented more favourable nival conditions for caribou. Trails and lowlands were also negatively associated with coniferous forests (Figure 2) where forages are more meagre and which female caribou typically have avoided at the broad scale in Newfoundland (Schaefer *et al.* 2016). We surmise that these spatial associations account for the apparent, broad-scale “preference” for snowmobile trails (Table 3).

Patterns of selection, however, may change across scales (Schaefer and Messier 1995; Mayor *et al.* 2009). Within their home ranges, GMNP caribou switched to preference for coniferous forests, a possible reflection of thinner snowcover in the midst of a denser canopy (Schaefer 1996). At this fine scale, they also did not avoid trails near the coast (Table 3),

where snowmachine activity was greatest (S. Taylor, personal observations), implying that snowmobiles and their trails did not represent a major limitation to GMNP caribou. Such observations still need to be viewed cautiously. Indeed, the counterfactual, how caribou would be distributed in the absence of snowmachine activity and trails, cannot be wholly known – a feature that our study shares with numerous other observational studies. Caution is warranted when anthropogenic disturbances are spatially associated with other landscape features (Schaefer and Mahoney 2007). Such ecological complexity underscores the value of experimental approaches, such as Before-During-After (Mahoney and Schaefer 2002) and replicated Before-After Control-Impact designs (Stewart-Oaten and Bence 2001). We agree with Hurlbert (1984:190) that “an experiment is

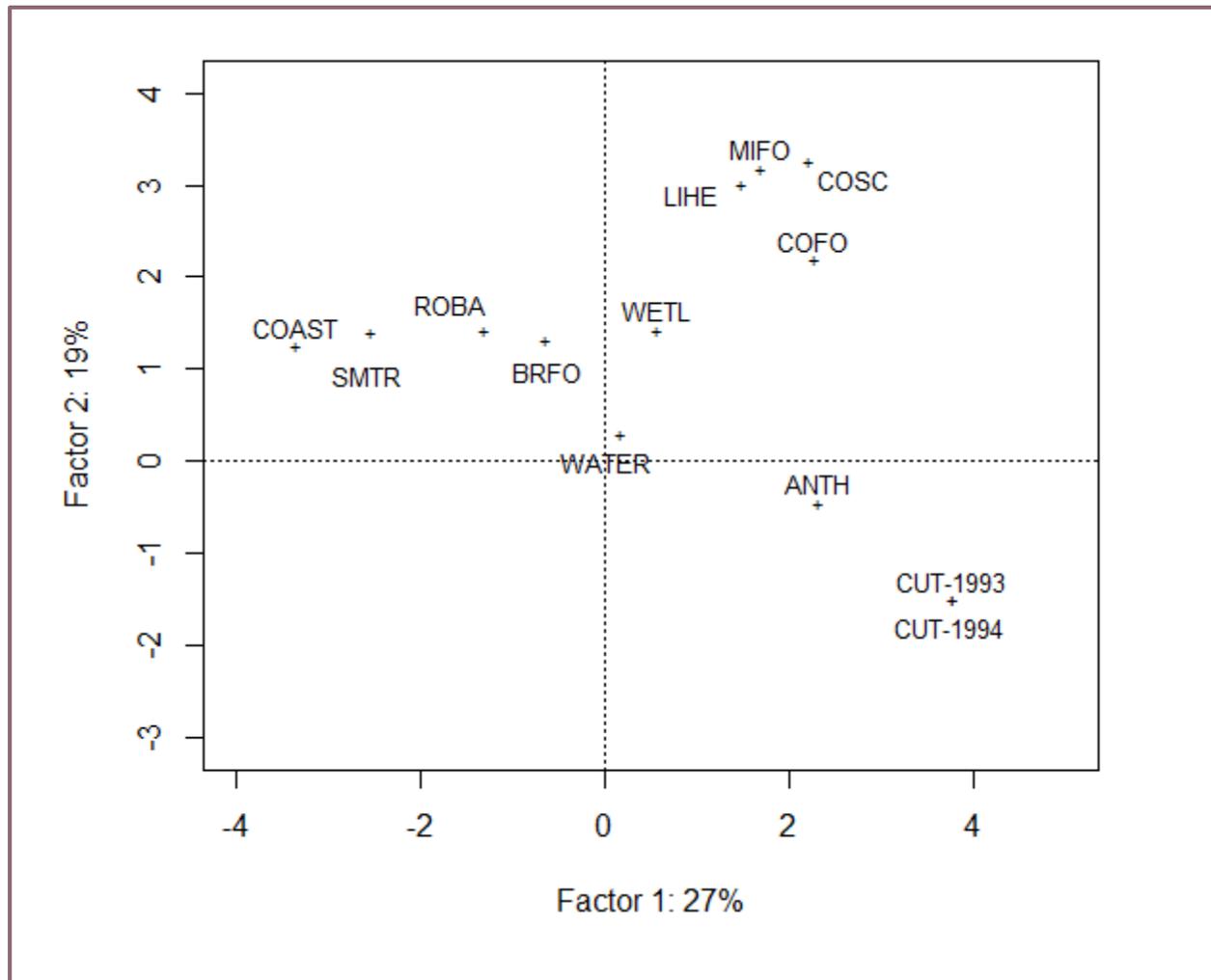


Figure 2. Scores on the first 2 axes of Principal Components Analysis showing the spatial relationships among habitat classes in Gros Morne National Park, Newfoundland. The percentage of variance explained is shown for each axis. See Table 3 for habitat acronyms.

successful to the extent that [confounding] factors are prevented from rendering its results inconclusive or ambiguous.”

Considerable differences exist among studies of the effects of snowmobiles on *Rangifer*. Apart from the common, short-term flight responses (Tyler 1991; Mahoney *et al.* 2001; Powell 2004), caribou may avoid or abandon areas of high snowmachine use (Seip *et al.* 2007). These divergent outcomes might be ascribed to several differences between studies. First, caribou in GMNP may be habituated to snowmachines, given the pervasiveness of trails, coupled with their predictable, regular, and (we assume) responsible use (Tyler 1991; Reimers *et al.* 2003). In contrast,

snowmachine use in British Columbia was intensive and not confined to trails (D. R. Seip, 2016, personal communication). Second, unlike Seip *et al.* (2007), GMNP caribou did not have access to an area where snowmachine activity was largely absent. Third, GMNP caribou were likely more food-limited (Schaefer *et al.* 2016) than the predator-limited sedentary ecotype (Bergerud 1980, Bergerud *et al.* 2008); GMNP females may have exhibited greater tendency for risk-prone foraging behaviour (Bastille-Rousseau *et al.* 2016). The contrasting results between our study and Seip *et al.* (2007) further underscores the need for rigorous, planned experiments.

Table 4. Estimated average energetic cost of single and multiple snowmachine disturbance events on caribou during winter, Gros Morne National Park, Newfoundland.

Cohort	Cost of a single disturbance event (COST, MJ/disturbance)	Winter mass loss (LOSS, kg) ¹	Energy equivalent of winter mass loss (ELOS, MJ)	Disturbance events causing 15% Mass Loss	Disturbance events causing 20% Mass Loss (EVNT)
Adult Male	0.14 - 0.16	5.3 – 21.1	190 - 758	1221 – 1341	> 2000
Adult Female	0.08 - 0.08	2.7 – 10.9	98 - 392	1189 – 1326	> 2000
Yearling Male	0.08 - 0.09	2.9 – 11.6	104 - 416	1192 – 1327	> 2000
Yearling Female	0.06 - 0.07	2.1 – 8.55	77 - 307	1176 – 1319	> 2000

¹ The amount of additional mass, lost due to disturbance events, required to produce a total of 15 or 20 % mass loss.

At the level of disturbance simulated in this study, with a snowmachine driving at 20 km/h (Mahoney *et al.* 2001), the direct energetic cost of encounters was negligible for caribou. Clearly, snowmachines moving at greater speeds might elicit a greater response (Tyler 1991; Stankowich 2008) but negligible energetic responses may result from predictable, frequent, and non-threatening events (Bergerud 1978; Geist 1978; Tyler 1991; Colman *et al.* 2001; Powell 2004, Harris *et al.* 2014). Indeed, even if an animal encountered a large number of the snowmachines (i.e., 41 encounters/day; Table 1), we estimate 58 days of exposure to induce threshold mass losses in yearlings and adults (Table 4). We do not suggest that large numbers of snowmachine encounters (e.g., 100) would have insignificant effects on caribou. Rather, in our study, the observed effects do not appear to be salient to the energy budget of GMNP caribou given the small behavioural response to low intensity provocation. More likely, substantial effects would be manifest through displacement or loss of foraging opportunities. Furthermore, we suggest higher energetic costs where caribou are subjected to irregular, unpredictable, or greater levels of disturbance than in GMNP, and where caribou may simply cease to use these areas rather than pay this cost (Harlow *et al.* 1987; Bradshaw *et al.* 1998; D. Seip, 2016, personal communication). Obviously, the relative energetic cost of disturbances would be greater for animals in poor condition – for instance, an adult that had already lost 14% of its body mass.

Our findings are consistent with Tyler (1991) and Reimers *et al.* (2003). The predicted energetic costs from snowmachine disturbance were low because the distances that caribou moved in response to provocation were low (Mahoney *et al.* 2001), as are caribou movement costs, even on snow (Fancy and White 1987; Boertje 1985). Our results stand in contrast to Bradshaw *et al.* (1998), however, who reported animals disturbed by petroleum exploration traveled much farther post-disturbance, but who also assumed a higher excitement cost in their model (45-67% of the total cost). Disturbance may affect animals in other ways – such as a rise in stress hormones or compensatory foraging – but studies to date suggest these influences are minor (e.g., Colman *et al.* 2003; Creel *et al.* 2009).

MANAGEMENT CONSIDERATIONS

Wildlife-snowmachine interactions are likely to continue to increase in North America. In the past 2 decades, snowmobiles have become bigger, faster, more reliable, and more numerous – for example, over 115,000 snowmobiles are registered in Newfoundland and Labrador, a province with a population of less than 550,000 people. In addition, adventure tourism is more prevalent in GMNP than in the 1990s (Taylor and Simpson 2005), including a substantial increase in the use of uplands in the Park (S. Taylor, personal observations). On the other hand, in GMNP, non-residents

are required to stay along corridors and residents are restricted from sensitive areas to protect unique, threatened, or endangered natural or cultural features. The Park may represent a best-case scenario for caribou in areas of high snowmachine activity.

The identification of limiting factors is central to wildlife management. Under conditions of frequent, predictable, and low-intensity disturbance, snowmachines appear not to represent a major limitation to GMNP caribou. They have little influence on caribou energetics. At least in the lowlands of this Park, female caribou use habitat in close proximity to snowmachine trails, implying that other factors (such as relative forage abundance) may be more salient. Displacement of caribou appears to result from intensive, widespread snowmobile use (Seip *et al.* 2007); this implies that restricting snowmachines to trails may confine the area of disturbance and may increase its predictability for caribou.

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LITERATURE CITED

- Adamczewski, J. Z., R. J. Hudson, and C. C. Gates. 1993.** Winter energy balance and activity of female caribou on Coats Island, Northwest Territories: the relative importance of foraging and body reserves. *Canadian Journal of Zoology* 71: 1221–1229.
- Bastille-Rousseau, G., J. A. Schaefer, S. P. Mahoney, D. L. Murray. 2013.** Population decline in semi-migratory caribou (*Rangifer tarandus*): intrinsic or extrinsic drivers? *Canadian Journal of Zoology* 91: 820–828.
- Bastille-Rousseau, G., J. A. Schaefer, K. P. Lewis, M. A. Mumma, E. H. Ellington, N. D. Rayl, S. P. Mahoney, D. Pouliot, and D. L. Murray. 2016.** Phase-dependent climate-predator interactions explain three decades of variation in neonatal caribou survival. *Journal of Animal Ecology* 85: 445–456.
- Bergerud, A. T. 1978.** Caribou. Pages 83–101 in J. L. Schmidt and D. L. Gilbert, editors. *Big game of North America*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- Bergerud, A. T. 1980.** A review of population dynamics of caribou and wild reindeer in North America. Pages 556–581 in E. Reimers, E. Gaare, and S. Skjenneberg, editors. *Proceedings of the 2nd International Reindeer/Caribou Symposium*. Direktoratet for vilt og ferskvannsfisk, Trondheim, Norway.
- Bergerud, A. T., S. N. Luttich, and L. Camps. 2008.** The return of Caribou to Ungava. McGill-Queen's University Press, Montreal, Québec, Canada.
- Bingham, R. L., L. A. Brennan, and B. M. Ballard. 2010.** Discrepancies between euclidean distance and compositional analyses of resource selection data with known parameters. *Journal of Wildlife Management* 74: 582–587.
- Boertje, R. D. 1985.** An energy model for adult female caribou of the Denali Herd, Alaska. *Journal of Range Management* 38: 468–473.
- Boulanger, J., K. G. Poole, A. Gunn, and J. Wierzchowski. 2012.** Estimating the zone of influence of industrial developments on wildlife: a migratory caribou *Rangifer tarandus groenlandicus* and diamond mine case study. *Wildlife Biology* 18: 164–179.
- Bradshaw, C. J. A., S. Boutin, and D. M. Hebert. 1998.** Energetic implications of disturbance caused by petroleum exploration to woodland caribou. *Canadian Journal of Zoology* 76: 1319–1324.
- Cameron, R. D. 1983.** Issue: caribou and petroleum development in Arctic Alaska. *Arctic* 36: 227–231.
- Cameron, R. D., and J. M. Ver Hoef. 1994.** Predicting parturition rate of caribou from autumn body mass. *Journal of Wildlife Management* 58: 674–679.
- Colman, J. E., B. W. Jacobsen, and E. Reimers. 2001.** Summer response distances of Svalbard reindeer to provocation by humans on foot. *Wildlife Biology* 7: 275–283.
- Colman, J. E., C. Pedersen, D. Hjermann, O. Holand, S.R. Moe, and E. Reimers. 2003.** Do wild reindeer exhibit grazing compensation during insect harassment? *Journal of Wildlife Management* 67: 11–19.
- Conner, L. M. and B. W. Plowman. 2001.** Using Euclidean distances to assess nonrandom habitat use. Pages 275–290 in J. J. Millsapugh and J. M. Marzluff, editors. *Radio tracking and animal populations*. Academic Press, San Diego, California, USA.
- Conner, L. M., M. D. Smith, and L. W. Burger. 2003.** A comparison of distance-based and classification-based analyses of habitat use. *Ecology* 84: 526–531.

- Creel, S., J. A. Winnie Jr., and D. Christianson. 2009.** Glucocorticoid stress hormones and the effect of predation risk on elk reproduction. *Proceedings of the National Academy of Sciences* 106: 12388-12393.
- Dauphiné, T. C., Jr. 1976.** Biology of the Kaminuriak population of barren-ground caribou. Part 4: growth, reproduction and energy reserves. Canadian Wildlife Service Report Series No. 38, Ottawa, Ontario, Canada.
- Dustin, D. L., and I. E. Schneider. 2005.** The science of politics/the politics of science: examining the snowmobile controversy in Yellowstone National Park. *Environmental Management* 34: 761-767.
- Eckstein, R. G., T. F. O'Brien, O. J. Rongstad, and J. G. Bollinger. 1979.** Snowmobile effects on movements of white-tailed deer: a case study. *Environment and Conservation* 6: 45-51.
- ESRI 2014.** ArcGIS Desktop: Release 10.1. Redlands, CA: Environmental Systems Research Institute.
- Fancy, S. G. 1986.** Daily energy budgets of caribou: a simulation approach. PhD thesis, University of Alaska, Fairbanks, USA.
- Fancy, S. G., and R. G. White. 1985.** Energy expenditures by caribou while cratering in snow. *Journal of Wildlife Management* 49: 987-993.
- Fancy, S. G., and R. G. White. 1987.** Energy expenditures for locomotion by barren-ground caribou. *Canadian Journal of Zoology*. 65: 122-128.
- Freddy, D. J., W. M. Bronaugh, and M. C. Fowler. 1986.** Responses of mule deer to disturbance by persons afoot and snowmobiles. *Wildlife Society Bulletin* 14: 63-68.
- Geist, V. 1978.** Behavior. Pages 283-296 in J. L. Schmidt and D. L. Gilbert, editors. *Big game of North America*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- 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
- Hagemoen, R. I. M., and E. Reimers. 2002.** Reindeer summer activity pattern in relation to weather and insect harassment. *Journal of Animal Ecology* 71: 883-892.
- Harlow, J. J., E. T. Thorne, E. S. Williams, E. L. Belden, and W. A. Gern. 1987.** Adrenal responsiveness in domestic sheep (*Ovis aries*) to acute and chronic stressors as predicted by remote monitoring or cardiac frequency. *Canadian Journal of Zoology* 65: 2021-2027.
- Harris, G., R. M. Nielson, T. Rinaldi, and T. Lohuis. 2014.** Effects of winter recreation on northern ungulates with focus on moose (*Alces alces*) and snow mobiles. *European Journal of Wildlife Research* 60:45-58.
- Hudson, R. J. and R. J. Christopherson. 1985.** Maintenance metabolism. Pages 122-137 in R. J. Hudson and R. G. White, editors. *Bioenergetics of Wild Herbivores*. CRC Press, Inc., Boca Raton, Florida, USA.
- Hudson, R. J., and R. G. White. 1985.** Computer simulation of energy budgets. Pages 261-290 in R. J. Hudson and R. G. White, editors. *Bioenergetics of Wild Herbivores*. CRC Press, Inc., Boca Raton, Florida, USA.
- Integrated Informatics, Inc. 2013.** An ecological land cover of Newfoundland for caribou based on LANDSAT imagery. Report to Government of Newfoundland and Labrador, St-John's, Newfoundland, Canada.
- Johnson, D. H. 1980.** The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65-71.
- Loison, A., R. Langvatn, and E. J. Solberg. 1999.** Body mass and winter mortality in red deer calves: disentangling sex and climate effects. *Ecography* 22: 20-30.
- MacArthur, R. A., R. H. Johnston, and V. Geist. 1979.** Factors influencing heart rate in free-ranging bighorn sheep: a physiological approach to the study of wildlife harassment. *Canadian Journal of Zoology* 57: 2010-2021.
- Mahoney, S. P., K. Mawhinney, C. McCarthy, D. Anions, and S. Taylor. 2001.** Caribou reactions to provocation by snowmachines in Newfoundland. *Rangifer* 21: 35-44.
- Mahoney, S. P. and J. A. Schaefer. 2002.** Hydroelectric development and the distribution of migration in caribou. *Biological Conservation* 107: 147-153.
- Mawhinney, K., S. P. Mahoney, C. McCarthy, S. Taylor, and D. Anions. 1998.** Caribou ecology and snowmachine disturbance in Gros Morne National Park. 1998 Summary Report. Parks Canada Report. Contract No. GRM97-002.
- Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009.** Habitat selection at multiple scales. *Écoscience* 16: 238-247.
- McEwan, E. H. 1970.** Energy metabolism in barren ground caribou (*Rangifer tarandus*). *Canadian Journal of Zoology* 48: 391-392.
- Moen, A. N., S. Whitmore, and B. Buxton. 1982.** Effects of disturbance by snowmobiles on heart rate of captive white-tailed deer. *New York Fish and Game Journal* 29: 177-183.
- Morehouse, A. T. and M. S. Boyce. 2013.** Deviance from truth: telemetry location errors erode both precision and accuracy of habitat-selection models. *Wildlife Society Bulletin* 37: 596-602. doi:10.1002/wsb.292
- Nellemann, C. and R. D. Cameron. 1998.** Cumulative impacts of an evolving oil-field complex on the distribution of calving caribou. *Canadian Journal of Zoology* 76: 1425-1430.
- Nellemann, C., P. Jordhøy, O-G Støen, and O. Strand. 2000.** Cumulative impacts of tourist resorts on wild

- reindeer (*Rangifer tarandus tarandus*) during winter. *Arctic* 53: 9-17.
- Obbard, M. E., M. B. Coady, B. A. Pond, J. A. Schaefer, and F. G. Burrows. 2010.** A distance based-analysis of habitat selection by American black bears (*Ursus americanus*) on the Bruce Peninsula, Ontario, Canada. *Canadian Journal of Zoology* 88: 1063-1076.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2013.** *Vegan: Community Ecology Package*. R package version 2.0-10. <http://CRAN.R-project.org/package=vegan>
- Olliff, T., K. Legg, and B. Kaeding. 1999.** Effects of winter recreation on wildlife of the Greater Yellowstone Area: a literature review and assessment. Report to the Greater Yellowstone Coordinating Committee. Yellowstone National Park, Wyoming USA.
- Polfus, J. L., M. Hebblewhite, and K. Heinemeyer. 2011.** Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. *Biological Conservation* 144: 2637-2646.
- Powell, T. 2014.** Réponse comportementale des caribous des bois au harcèlement par les motoneiges. MSc thesis, Université de Sherbrooke, Québec, Canada.
- Pruitt, W. O., Jr. 1959.** Snow as a factor in the winter ecology of the barren ground caribou (*Rangifer arcticus*). *Arctic* 12: 158-179.
- R Core Team. 2013.** R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Reid, C. 1993.** Over snow vehicle data collection 1993. Internal Report. Gros Morne National Park, Newfoundland, Canada.
- Reid, C. 1994.** Over snow vehicle data collection 1993. Internal Report. Gros Morne National Park, Newfoundland, Canada.
- Reimers, E. and J. E. Colman. 2006.** Reindeer and caribou (*Rangifer tarandus*) response towards human activities. *Rangifer* 26: 55-71.
- Reimers, E., S. Eftesol, and J. E. Colman. 2003.** Behavior responses of wild reindeer to direct provocation by a snowmobile or skier. *Journal of Wildlife Management* 67: 747-754.
- Schaefer, J. A. 1996.** Canopy, snow, and lichens on woodland caribou range in southeastern Manitoba. *Rangifer*, Special Issue 9: 239-244.
- Schaefer, J. A., and S. P. Mahoney. 2007.** Effects of progressive clearcut logging on Newfoundland caribou. *Journal of Wildlife Management* 71: 1753-1757.
- Schaefer, J. A., and S. P. Mahoney. 2013.** Spatial dynamics of the rise and fall of caribou (*Rangifer tarandus*) in Newfoundland. *Canadian Journal of Zoology* 91: 767-774.
- Schaefer, J.A., S. P. Mahoney, J. N. Weir, J. G. Luther, and C. E. Soulliere. 2016.** Decades of habitat use reveal food limitation of Newfoundland caribou. *Journal of Mammalogy* 97: 386-393.
- Schaefer, J. A., and F. Messier. 1995.** Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography* 18: 333-344.
- Seip, D. R., C. J. Johnson, and G. S. Watts. 2007.** Displacement of mountain caribou from winter habitat by snowmobiles. *Journal of Wildlife Management* 71: 1539-1544.
- Shank, C. C. 1979.** Human-related behavioral disturbance to large northern mammals: a bibliography and review. Report prepared for Foothills Pipe Lines (South Yukon) Ltd, Calgary, Alberta, Canada.
- Shideler, R. T., H. H. Robus, J. J. Winters, and M. Kuwada. 1986.** Impacts of human developments and land use on caribou: a literature review, Volume I. A worldwide perspective. Technical Report, 86-3. Alaska Department Fish and Game Division Habitat, Alaska, USA.
- Sikes, R.S., Gannon, W. L., and the Animal Care and Use Committee of the American Society of Mammalogists. 2011.** Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92: 235-253.
- Stankowich, T. 2008.** Ungulate flight responses to human disturbance: a review and meta-analysis. *Biological Conservation* 141:2159-2173.
- Steen, E. 1968.** Some aspects of the nutrition of semi-domestic reindeer. *Symposia of the Zoological Society of London*. 21: 117-128.
- Stewart-Oaten, A., and J. R. Bence. 2001.** Temporal and spatial variation in environmental impact assessment. *Ecological Monographs* 71: 305-339.
- Taylor, S., and A. Simpson. 2005.** Determining the patterns of use of snowmobilers in Gros Morne National Park, Winter 2005. Internal Report. Gros Morne National Park, Newfoundland, Canada.
- Thomas, D. C., R. H. Russell, E. Broughton, and P. L. Madore. 1976.** Investigations of Peary caribou populations on Canadian Arctic islands, March - April 1975. *Canadian Wildlife Service Progress Note* No. 64.
- Tyler, N. J. C. 1991.** Short-term behavioural responses of Svalbard reindeer *Rangifer tarandus platyrhynchus* to direct provocation by a snowmobile. *Biological Conservation* 56: 179-194.

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

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.

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

Wulder, M. A., J. C. White, S. N. Goward, J. G. Masek, J. R. Irons, M. Herold, W. B. Cohen, T. R. Loveland, and C. E. Woodcock. 2008. Landsat continuity: issues and opportunities for land cover monitoring. *Remote Sensing of Environment* 113: 955-969.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

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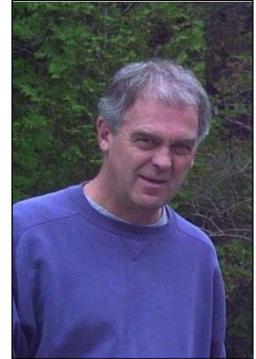
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