The 12th North American Caribou Workshop, Happy Valley/Goose Bay, Labrador, Canada, 4–6 November, 2008.

Land management strategies for the long-term persistence of boreal woodland caribou in central Saskatchewan

A. Alan Arsenault¹ & Micheline Manseau²

¹ AMEC Earth & Environmental, 4015 Millar Avenue, Saskatoon, Saskatchewan, Canada S7K 2K6. (Formerly, Saskatchewan Ministry of Environment, 112 Research Drive, Saskatoon, Saskatchewan, Canada S7K 2H6).

² Parks Canada Agency, 145 McDermot Ave., Winnipeg, Manitoba, Canada R3B 0R9 (corresponding author: Micheline. Manseau@pc.gc.ca) and University of Manitoba, Natural Resources Institute, 70 Dysart Road, Winnipeg, Manitoba, Canada R3T 2N2.

Abstract: We investigated landscape changes and their potential effects on woodland caribou-boreal ecotype (Rangifer tarandus caribou) within a portion of the Smoothstone-Wapaweka Woodland Caribou Management Unit (SW-WCMU). The SW-WCMU is one of eight areas delineated by the Province of Saskatchewan for potential recovery planning efforts for boreal caribou, and is one of four management units located on the Boreal Plain Ecozone. The Prince Albert Greater Ecosystem (PAGE) study area was selected within the SW-WCMU for intensive study from 2004 - 2008. Studies focused on quantifying a suite of landscape and population parameters. This paper presents a summary of study results to date and recommends land management strategies intended to contribute to the long-term viability of boreal caribou in the central boreal plain ecoregion of Saskatchewan. The PAGE study area has undergone structural changes from an area that historically presented a lesser amount but well connected mature coniferous forest, to a currently larger amount of mature coniferous stands fragmented by a highly developed network of roads and trails. Movement data pointed to highly clustered use of the landscape by small groups of caribou and smaller home ranges when compared to 15 years ago. Calving sites were located within each individual home range in treed peatland and distant from hardwood/mixedwood forest stands, roads and trails access. Adult annual survival rates were low, averaging 73% over the course of the study. In order to ensure a self-sustaining population level, study results clearly point to the need for landscape restoration to reduce the level of anthropogenic disturbances in some key parts of the study area. Key strategies include retention of mature softwood forest interior proximate to local areas of caribou activity, protection of calving habitat, improving structural connectivity, planning disturbances (forest harvesting, fire salvage, resource exploration, access development) in ways to minimize the anthropogenic footprint, and recovery action planning integrated with other land-use planning initiatives.

Key words: boreal woodland caribou; ecological integrity; habitat connectivity; habitat selection; land management strategies; non-invasive genetic sampling; Saskatchewan.

Rangifer, Special Issue No. 19: 33-48

Introduction

The approach to ecologically-based land management strategies for boreal caribou in Canada are outlined in the national recovery strategy (Environment Canada, 2007). Specifically, each jurisdiction within Canada with boreal caribou agreed that recovery efforts should occur at the range level because caribou populations have broad landscape-level habitat requirements. The range of a given caribou population contains a variety of habitat components that are differentially used, as well as the intervening landscape matrix. Sorensen et al. (2008) demonstrated a strong relationship between population growth rates and the amount of natural and anthropogenic disturbance. They also identified landscape disturbance thresholds above which population growth rate would likely be declining. Numerous documents have been prepared at the provincial/territorial level detailing best management practices, industrial operating guidelines, and landscape management planning processes that will serve as the basis for boreal caribou recovery action planning efforts across the country (Environment Canada, 2007).

Habitat strategies focus on defining the types and amounts of natural and anthropogenic activities that can occur on the landscape to ensure that populations are self-sustaining, or growth rates are either stable or increasing. This entails looking at the habitat quantity, quality and spatial configuration within a range (Environment Canada, 2008), the amount and configuration of selected habitat types in relation to burn areas, younger forests, and industrial development such as linear features which have the potential to reduce caribou population viability and lead to an increased abundance of other cervid species such as white-tailed deer (Odecoileus virginianus), elk (Cervus elaphus) and moose (Alces alces), as well as their associated predators such as grey wolf (Canis lupus) and black bear (Ursus americanus) thereby influencing predator-prey dynamics, resource selection functions, and boreal forest integrity (Cundiff & Gray, 2004; Environment Canada, 2007).

Currently in Saskatchewan there is limited integration between caribou conservation planning and land management processes such as the area specific land-use planning process on sensitive landscapes, project specific environmental assessment, review and screening process (subject to *The Environmental Assessment Act 1980*, best management practices (SMEGAC, 2007), set-back distance recommendations (SKCDC, 2003; Arsenault, 2009), and forest management agreements governing commercial forest harvesting (subject to *The Forest Resources Management Act, 1996*). This is due in part because boreal caribou have not yet been formally listed in provincial legislation as a species at risk. Saskatchewan Ministry of Environment (2009) is developing natural forest pattern standards and guidelines for the forest industry, which are intended to produce landscapes and harvest areas that look and function like landscapes and disturbance patches created by natural disturbances such as fire. Ultimately, a recovery action plan for the Smoothstone-Wapaweka Woodland Caribou Management Unit (SW-WCMU) must have direct linkage to an effective and integrated decision-making process for land management, subject to the appropriate provincial and federal legislation.

Prince Albert National Park (PANP) land management focuses on maintaining ecological processes and functions within the park, as well as integration of efforts with adjacent land-use activities that potentially impact the park's ecological integrity and native biological diversity. Boreal caribou still reside in the Prince Albert National Park Greater Ecosystem (PAGE), but there is concern that management activities within PANP, and in the adjacent forested landscape surrounding the park, are compromising the ecological integrity of the PAGE landscape and the ability for boreal caribou to persist as a viable component of this portion of the Boreal Plain Ecosystem over the long-term. Consequently, in 2004, the Western and Northern Service Centre of Parks Canada, Prince Albert National Park, Saskatchewan Environment, University of Manitoba Natural Resources Institute, Prince Albert Grand Council, Prince Albert Model Forest, Weyerhaeuser Canada Ltd. and the National Resources DNA Profiling and Forensic Centre at Trent University formed a collaborative research partnership to collect data needed to determine measures of landscape connectivity for appropriate land management planning that would ensure boreal caribou remain a viable component of the PAGE landscape. The PAGE study area is situated within the SW-WCMU. The study focused on obtaining population and landscape parameters. Population parameters were obtained through a collaring program and DNA analysis, and landscape parameters were obtained through mapping and ground truthing activities, which were used to produce decadal landcover maps for the period of 1947-2007, resource selection function models, and predictive habitat maps for both summer and winter. The models were structured around habitat quality attributes (including spatial and temporal anthropogenic and natural disturbance), lichen productivity, optimal foraging strategies, and predator avoidance strategies. Time-series analyses were used to assess landscape changes over time. Spatial graph theory

Table 1.	Summary	of	research	proi	ects	primary	focus	and	research	lead
rable r.	Summary	OI	rescaren	proj	ccco,	primary	rocus	and	rescaren	neau.

Projects	Authors				
Landscape changes and decadal landscape reconstruction.	Arlt, 2009; Arlt & Manseau, 2011				
Delineate Saskatchewan caribou range by integrating information sources.	Arsenault, 2003; Saskatchewan Environment, 2007				
Telemetry study of movement rate and seasonal habitat use patterns.	Dyke, 2008; Koper & Manseau, 2009				
Quantification of range size and distribution changes over the past decade.	Arlt & Manseau, 2011				
Changes in landscape connectivity.	Fall et al., 2007; Arlt, 2009; Galpern et al., 2010				
Caribou calving site selection.	Dyke, 2008				
Population genetic structure and gene flow.	Ball, 2008; Ball et al., 2010				
Fecal-DNA based capture-mark – recapture population size estimates.	Hettinga et al., 2010; Hettinga (unpubl. results)				

models (Fall & Fall, 2001; O'Brien *et al.*, 2006; Fall *et al.*, 2007; Galpern *et al.* 2010) were used to assess habitat connectivity and to project future scenarios based on changes to available habitat and landscape connectivity, including the implications to boreal caribou.

A non-invasive DNA sampling technique was furthered by collecting winter caribou fecal samples in the PAGE study area. The purpose of this study was to determine relatedness of caribou populations across broad landscape scales (i.e. landscape connectivity at the SW-WCMU level), to assess genetic diversity at the population level, and to attempt estimation of population size through fecal-DNA based mark-recapture methods (Hettinga *et al.*, 2010) within the PAGE study area.

The PAGE project was multi-faceted, employing multiple methods in related studies with several project objectives. This paper integrates all available information collected in the SW-WCMU, and presents a summary of key results. Table 1 provides a summary of the research projects, primary focus and lead authors. Based on study results, land management strategies are proposed to ensure that sufficient habitat is available for the long-term viability of boreal caribou in central Saskatchewan.

Boreal caribou in Saskatchewan

Arsenault (2003; 2005) compiled a comprehensive geospatial coverage of boreal woodland caribou location data for Saskatchewan dating back to 1950. Data sources included that from Arsenault (1984-present, unpubl. data), Saskatchewan Government historical survey data and incidental observations, PAGC (2002), Prince Albert National Park (unpubl. historical data), Trottier (1988) and Rettie (1998). The coverage provides context for assessing historical caribou distribution, and was used to delineate local population occurrence (Fig. 1). The information used included documented observations of caribou from aerial surveys, incidental sightings, telemetry data, and local knowledge (Arsenault, 2003; 2005; Saskatchewan Environment, 2007) (Fig. 1). Eight WCMUs (Fig. 1) were then delineated by encompassing clusters of caribou location data and peatland distribution on ecologically similar areas, as defined by Acton et al. (1998). Four of the WCMUs occur on the Boreal Shield Ecozone and four occur on the Boreal Plain Ecozone. Each WCMU represents an ecologically delineated portion of the provincial caribou range for the purpose of monitoring and assessing caribou populations and managing land-use activities impacting them. WCMUs were used as a base for developing directed studies, for recovery and landscape planning in Saskatchewan (Saskatchewan Environment, 2007), and as part of the national recovery strategy development (Environment Canada, 2007).

A local population has been defined as a group of potentially interbreeding individuals at a given locality (Mayr, 1963; Cronin, 2003). A local caribou population in Saskatchewan is defined as a geographically distinct association of potentially interacting and interbreeding individuals occupying a discrete area of suitable habitat, with recurring history of use as demonstrated through the historical location data (Arsenault, 2003; Saskatchewan Environment, 2007) (Fig.1). Environment Canada (2008) describe a local population as distinguished spatially from areas occupied by other local populations, experience limited exchange of individuals with other local populations such that population dynamics are primarily driven by local factors affecting birth and death rates, rather than immigration and emigration. At the landscape scale, the spatial extent and degree of isolation of local populations affects the WCMU population through the dynamics of its recruitment system, effects on population growth through immigration and emigration, dispersal movement among local populations, influxes from other WCMUs, and distribution pattern on the landscape (Thomas & Kunin, 1999; Steen & Haydon, 2000; Berryman, 2002; Camus & Lima, 2002; Baguette & Stevens, 2003; Schaefer, 2006). As additional work is done in the SW-WCMU and detailed information on population structure becomes available, the current local population boundaries (Fig. 1) may be altered. Environment Canada (2009) has identified potential criteria for subdividing contiguous caribou distribution into local population ranges based on animal movement data and where less than 10% emigration and immigration occurs among groups of animals.

Woodland Caribou Management Units

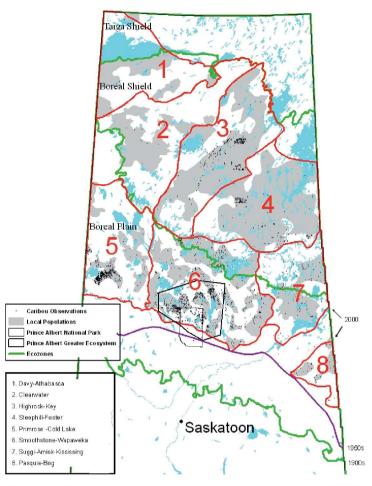


Fig. 1. PAGE Study Area and woodland caribou management units (WCMU – red), indicating local population ranges and range contraction based on data compiled from 1900 (green), 1950 (purple) to present (red) (source: Arsenault, 2003; Saskatchewan Environment, 2007).

Study area

The PAGE study area (Fig. 2) was 13 381 km² in size, located in the central part of the Boreal Plain Ecoregion within the SW-WCMU (Fig. 1). PANP is central to the PAGE study area and represents a transition zone between the aspen parkland and the boreal forest. This is the only location in Canada where freeranging plains bison occur within their natural range as part of the compliment of endemic cervid species (Arsenault, 2005). Within the SW-WCMU, elk, white-tailed deer and mule deer occur in the highest densities at the interface of the aspen parklandfarmland and the provincial crown forest, diminishing northward. Moose are found at higher densities in proximity to regenerating clear-cuts throughout the area (Arsenault, 2009). This has implications for the number and distribution of natural predators and for caribou distribution. Within the SW-WCMU, the size and distribution of local caribou populations increases northward.

Caribou populations within the SW-WCMU appear to have fluctuated during the last 60 years. Rock (1992) reported a decline in woodland caribou during the mid-1940s resulting in closure of the hunting season in 1946. This was followed by an increase in the late 1950s attributed to the hunting season closure and a wolf control program (Rock, 1992). Regulated caribou hunting resumed in a portion of the north in 1961, but low harvest levels resulted in closure of the hunting season in 1987. In PANP, a 1939-1940 census of caribou indicated an overwinter population of 600-700 (Soper, 1951). Banfield later reviewed Soper's data and down-graded the estimate to 200 animals, and estimated the 1951 population to be 50 (Rock, 1992). Over the next 25 years, survey efforts reported 24 caribou in 1970-71, 37 in 1977, and 26 in 1978 (Burles *et al.*, 1978). Very few sightings of caribou have been reported in the park since, despite significant survey and collaring efforts (Arlt & Manseau, 2011).

Wildfires have occurred throughout much of the study area to varying degrees and sizes over recent decades along with fire suppression. Recent burns have occurred in the Bittern Lake area east of PANP and in the northeast section of PANP. Access has dramatically increased in relation to development and forestry, with resultant increases in vehicular and off-road traffic for recreation (snow mobiles, all-terrain vehicle use, cross-country skiing, hiking, boating, cottages, etc.), hunting, fishing, trapping, resource extraction, and travel among communities. Weyakwin, Ramsay Bay on Weyakwin Lake, Timber Bay, reserve

communities of Montreal Lake First Nation and Lac la Ronge Indian Band (Bittern Lake), Waskesiu and seasonal resorts east of PANP are settlements within the PAGE study area. Dore Lake and Sled Lake are additional small settlements adjacent to the PAGE study area. There is significant variation across the SW-WCMU in terms of habitat mosaic, anthropogenic footprint, and species distribution. Therefore, application of landscape management strategies will vary spatially depending on the characteristics of the particular area.

Results

Landscape changes

A land cover map consisting of 20 vegetation classes was developed for the PAGE study area using forest resource inventory data obtained from PANP, Weyerhaeuser Canada Ltd. and the Saskatchewan Government. Using this land cover map, the PAGE landscape was reconstructed for each decade from 1946 – 2006 to document changes in land cover

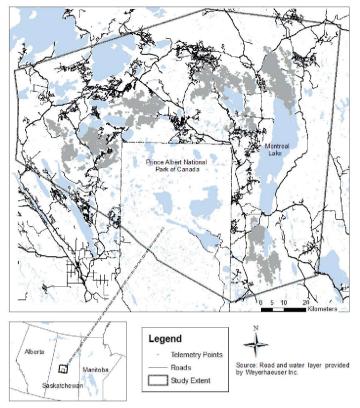


Fig. 2. Map of the Prince Albert Greater Ecosystem highlighting anthropogenic features and telemetry data from 28 female caribou between 2004-2008.

types, the development of linear features, the occurrence of logging activities and wildfire (Arlt, 2009; Arlt & Manseau, 2011). Transition probabilities analyses showed that the PAGE landscape was historically characterized by a high wildfire frequency with a greater proportion of younger aged coniferous stands and marginal access development for forest harvesting activities. The current PAGE landscape has larger proportions of mature coniferous stands because of fire suppression and ecological succession. Many of these stands have been modified outside of PANP primarily by forest harvesting activities, wildfires, wildfire suppression with salvage logging, and linear development (roads, trails, power corridors). The landscape has a high density of linear features with about 20% of the area logged or comprised of hardwood dominated forest stands (Arlt, 2009; Arlt & Manseau, 2011). The cumulative area logged in the PAGE increased from essentially nil between 1956 and 1976 to 58 211 ha (4.4 ha/km²) by 2006. During this same period cumulative permanent road/trail development within the PAGE increased from about

342 km in 1956 to almost 4730 km (0.35 km/km²) by 2006 (Arlt & Manseau, 2011). The PAGE area was assessed using the landscape disturbance threshold equation presented in Sorensen et al. (2008), which calculates population rate of change (λ) in relation to the amount of natural and human disturbance on the landscape. We obtained a λ of 1.06 when the amount of disturbance was calculated as a proportion of the entire PAGE study area, 1.03 when based on a study area excluding PANP and 1.17 when based on the extent of caribou home ranges. This suggests that the PAGE population should be growing, but our study results do not support this.

Caribou distribution

Over the course of the PAGE study, a total of 28 adult female caribou were fitted with #4400 GPS telemetry collars (Lotek Wireless Inc., Newmarket, Ontario) to monitor survival rates, movement and landscape use patterns at fine temporal and spatial scales (3 hr relocation frequency). Flights were conducted periodically to upload location data, to adjust collar data collection schedules, and to monitor mortality. Collars from dead caribou and collars nearing the end of their battery life were retrieved and refurbished annually, and redeployed to attempt to maintain a minimum of 15 collars on females across the PAGE study area. The telemetry data was used to assess caribou distribution, movement rate and seasonal habitat use patterns (Dyke, 2008; Koper & Manseau, 2009; Arlt & Manseau, 2011). Lastly, PAGE telemetry data was compared to that collected in an overlapping area by Rettie (1998) and Rettie & Messier (1998; 2001) in 1992-1995, to quantify changes in range size and distribution over the last decade.

In a previous study within SW-WCMU, Rettie & Messier (1998) reported a spatially disjunct distribution which is consistent with range contraction and local boreal caribou occupancy data reported by Arsenault (2003) and with current telemetry data. Current telemetry data was used to determine minimum convex polygons (MCP) of individual ranges. The analysis revealed that the PAGE animals are sedentary, with individual summer and winter ranges overlapping, with range occupancy being comparable between the two studies, but with individual home range sizes being significantly smaller (t = -2.559, P = 0.013, df = 52) for the 2004-2008 telemetry data (MCP: $\bar{x} = 221 \text{ km}^2$, s.d. = 145, n = 23), compared to the 1992-1995 telemetry data (MCP: $\bar{x} = 441 \text{ km}^2$, s.d. = 393, n = 31).

Telemetry and genetic results from the PAGE study also confirmed that the boreal caribou population has a fragmented distribution with limited use of PANP. Multi-year GPS telemetry data (2004-2008) for the PAGE study demonstrated that animals have a clustered distribution (Fig. 2), small annual home ranges ($\bar{x} = 221 \text{ km}^2$, s.d. = 145), low hourly movement rates ($\bar{x} = 122 \text{ m/hr}$, s.d. = 249) when compared to other caribou studies, no detected movement between groups, and with calving sites located throughout the landscape within each individual home range. This contrasts with other caribou studies where individual home ranges overlap and calving sites are clustered (Dyke, 2008).

Caribou calving sites

Dyke (2008) used fine scale telemetry movement data from the PAGE study to look at the spatial and temporal characteristics of animal movement during the calving period. Dyke (2008) identified calving caribou if they presented a reduction of adult cow movement rates to <50 m/hr for a minimum of a week, which corresponded to a highly defined location during the calving period (treated as a minimal number of animals calving). Dyke (2008) was able to determine a 29 April – 7 June calving season for PAGE caribou with almost 75% of calving completed by mid-May, which was similar to that reported elsewhere (Hirai, 1998; Schaefer et al., 2000; Lantin et al., 2003). Timing of calving is highly dependant on the presence of suitable forage species to ensure sufficient milk production (Rutberg, 1987; Post et al., 2003; Gustine et al., 2006). Dyke (2008) noted the occurrence of late calving could be attributed to fertilization in second estrous.

Animals that presented the calving behavior showed a high degree of spatial separation from conspecifics, which is consistent with that reported elsewhere (Bergerud *et al.*, 1984; Gustine *et al.*, 2006). The spatial clustering of areas used for pre-calving, calving and post-calving in the PAGE area was different from other caribou studies (Dyke, 2008), suggesting that calving site selection may be influenced by disturbances in the surrounding area (Gustine *et al.*, 2006; Dyke, 2008) and predation risk (Post *et al.*, 2003).

Boreal caribou generally show strong selection for black spruce stands within large treed peatlands (Hirai, 1998; Rettie & Messier, 2001; Lantin *et al.*, 2003), which is supported by Dyke's (2008) results. Calving females in the PAGE area demonstrated strong selection for treed peatlands, (particularly those further from mixed hardwood stands), and avoidance of mature jackpine stands, mixed hardwood stands, and roads during the calving period and in the spring – summer seasonal range (Dyke, 2008). However, when habitat was treated as a categorical variable in the analysis, both treed peatland and jackpine were selected. Habitat selection and avoidance patterns for PAGE caribou were similar to that reported in other boreal caribou populations (Ferguson *et al.*, 1988; Johnson *et al.*, 2003; Mahoney & Virgil, 2003; Brown *et al.*, 2007; Dyke, 2008), and for an earlier study of the PAGE area (Rettie & Messier, 2000). Dyke (2008) attributed the weaker selection of jackpine by PAGE caribou to the highly fragmented nature of jackpine stands and their proximity to hardwood mixedwood stands, young stands and roads.

Genetic structure and gene flow

Genetic diversity allows species to adapt to changing environmental conditions (Reed *et al.*, 1986). Isolation increases the probability of local extinction, reduction of population size, reduction in gene flow, and ultimately a decline in genetic health (loss of rare alleles, reduced heterozygosity, and inbreeding) (Reed *et al.*, 1986; Loew, 2000), which may affect the recovery of small meta-populations (Lacy, 1997; Lande, 2002; Arsenault, 2003).

The inbreeding coefficient (F_{is} value) ranges between -1.000 (outbreeding / heterozygote excess) and 1.000 (inbreeding / heterozygote deficiency). Based on a sample size of 78, the $F_{\scriptscriptstyle is}$ was calculated to be 0.061 with an expected heterozygosity $(F_{st EXP})$ of 0.76 ± 0.02 and observed heterozygosity ($F_{er,OBS}$) of 0.71±0.02 for the PAGE population (Ball, 2008; Ball et al., 2010). The genetic diversity of PAGE caribou within the SW-WCMU was similar to that reported in other populations (Côté et al., 2002; McLoughlin et al., 2004), with no apparent inbreeding or outbreeding issues. Isolation can result in disparate levels of genetic diversity that put populations at risk of local extinction if movement of adaptive alleles is not maintained by gene flow (Reed et al., 1986; Lacy, 1997; Ray, 2001; Lande, 2002; McLoughlin et al., 2004).

Population size and mortality rate

The minimum PAGE population based on identification of unique genotypes was 93 caribou, with preliminary results pointing to an estimate of 128 (95% 116, 145) animals (Hettinga, unpubl. results, Hettinga *et al.*, 2010). This yields a population density of 0.009 caribou/km² when calculated over the entire PAGE study area, and 0.11 caribou/km² when based on MCPs of annual home ranges.

Even minor increases in adult and/or calf mortality can cause a trend in population decline (Arsenault, 2003). This is because boreal caribou have a low reproductive rate (twinning is rare; cows commonly do not produce a calf annually) and they breed at relatively older ages compared to other cervids (McDonald & Martell, 1981; Godkin, 1986; Lavigueur & Barrette, 1992). Average annual adult survival rates of boreal caribou have been reported by Rettie & Messier (1998) in Saskatchewan (84%), McLoughlin et al. (2003) in northeast Alberta (83-93%), Brown et al. (2000) in Manitoba (90%), with mortality most common in summer (Rettie & Messier, 1998). Annual adult survival rates of collared PAGE caribou was 71% (2005, n=17), 71% (2006, n=17), 83% (2007, n=12), and 69% (2008, n=13), with a mean of 73% for all years pooled. The majority of mortalities occurred in summer, in June and August. Mortality features would have been more identifiable if the collars were retrieved immediately following receipt of the mortality signal. The high adult mortality rate suggests the population may be declining.

Calf survival to one year is usually low and varies temporally and spatially (Fuller & Keith, 1981; Edmunds, 1988; Adams et al., 1995). Typically only 30-50% of calves survive their first year of life (Thomas & Grav, 2001). We were not able to estimate calf survival. A non-spatial population viability analysis conducted by Arsenault (2007, unpubl. data) for Saskatchewan indicated a minimum recruitment of 31.4 calves/100 adult females (vearlings excluded) was required for a stable population based on mean annual adult female survival of 85% (Saskatchewan Environment, 2007). An independent critical habitat science review led by Environment Canada performed a similar analysis, concluding that a minimum recruitment rate of 28.9 calves/100 females was required (Environment Canada, 2008).

Discussion

Ecological considerations

The boreal forest landscape is naturally dynamic with specific habitat components having a functional role at different spatial and temporal scales which are necessary to assure persistence of local boreal caribou populations (Racey & Arsenault, 2007). In most impacted landscapes, the number, location and size of habitat patches, as well as the demographic parameters of the wildlife populations inhabiting them change temporally and spatially (Schaffer, 1981; Lande, 1988; Akcakaya, 2001; Mitchell, 2005). The influences of natural and anthropogenic landscape alteration and disturbance on caribou range use and occupancy includes documented range shifts following wildfire (Schaefer & Pruit, 1991), logging (Rettie & Messier, 1998; Smith et al., 2000; Lander, 2006; Schaefer & Mahoney, 2007; Vors et al., 2007), and industrial development (Dver et al., 2001; Nellemann et al., 2003; Weir et al., 2007), barrier and displacement effects of linear features (Rettie & Messier, 1998; Dyer et al., 2002; Schindler et al., 2007), increased predation risk (James, 1999; James & Stuart-Smith, 2000; James et al., 2004), and potentially increased energetic costs (Bradshaw et al., 1998). The degree of response to disturbance depends on the type, magnitude, frequency, and duration of the disturbance (Bradshaw et al., 1998; Arsenault, 2009). The impact of non-lethal human disturbance on the behaviour and reproductive success of animals can have a similar trade-off to predation, resulting in avoidance of perceived risk and other fitness enhancing activities such as feeding, parental care, or mating (Frid & Dill, 2002).

Assessing habitat use in relation to availability determines habitat selection (Bradshaw et al., 1995; Manly et al., 2002; Arsenault, 2003; Koper & Manseau, 2009). Habitat selection occurs at several scales, is variable, and reflects the strategies used by an animal to meet habitat requirements through selection of different environmental features at each level of spatial and temporal scale to optimize biological fitness (Johnson, 1980; Orians & Wittenberger, 1991; Holling, 1992; Bradshaw et al., 1995; Rettie & Messier, 2000; Arsenault, 2003; Johnson et al., 2004; Dussault et al., 2005; Lander, 2006; Dyke, 2008). Distribution and abundance of species-at-risk are adversely affected by changes in the land-use activities that cause habitat loss, habitat fragmentation, and other disturbances (Akcakaya, 2001). Small isolated local populations are subject to sudden extirpation by a stochastic event, or slow extinction due to accumulation of deleterious alleles through inbreeding (Reed et al., 1986). Local extinctions of fragmented populations are common; therefore, recolonization of local extinctions is critical for regional survival of fragmented populations (Fahrig & Merriam, 2002).

Understanding landscape connectivity in terms of habitat configuration and intervening covertypes in determining the degree to which a landscape facilitate or impedes movement among habitat patches is critical for determining ecological integrity, for effective landscape management, and for conservation of species-at-risk (Taylor *et al.*, 1993; Foreman, 1995; Tischendorf & Fahrig, 2000; Fahrig & Merriam, 2002; O'Brien *et al.*, 2006). An animal's ability to utilize a resource patch is dependent on its ability to get there. O'Brien *et al.* (2006) have shown the importance of landscape connectivity for woodland caribou and a strong selection for larger clusters of high quality habitat patches over the selection of a given high quality habitat patch. Habitat fragmentation isolates habitat patches and reduces patch size, thereby increasing the vulnerability of local populations to environmental and demographic threats (Shaffer, 1981; Lande, 1988). Boreal caribou are wide-ranging with natural occurrence at low population densities typically between 0.03 - 0.05 caribou/ km², and have protracted time lag responses to habitat changes (Tilman et al., 1994; Arsenault, 2003; Schaeffer, 2003; Environment Canada, 2007; Vors et al., 2007; Wilkinson, 2008). Therefore, studies that focus on landscape pattern analysis, as well as structural and functional habitat connectivity, are necessary to determine impact development thresholds, critical habitat, and movement corridors (Manseau et al., 2002; O'Brien et al., 2006; Fall et al., 2007; Racev & Arsenault, 2007; Galpern et al., 2010). Boreal caribou population declines are characterized by a loss of landscape connectivity accompanied by declines in population size and constrictions in local range occupancy, followed by a period of persistence of isolated populations exhibiting a slow decline culminating in local extirpation and range recession (Schaefer, 2003; Wilkinson, 2008).

Predation is the main factor limiting boreal caribou populations. Caribou have historically coexisted with wolves and other predators for thousands of years in a boreal forest ecosystem driven by natural disturbances such as wildfire. Boreal caribou sparsely distribute themselves and spatially separate from other prey species (commonly moose) into areas composed of habitats with very low densities of other prey species, as a predation-limiting strategy (Bergerud *et al.*, 1984; Bergerud, 1992; Seip, 1992).

In the Boreal Plain Ecozone caribou commonly select upland mature and old-growth jackpine and lichen-rich treed peatland complexes interspersed in mature and old growth black spruce forest (Brown et al., 2000b; Rettie & Messier, 2000; Schneider et al., 2000; Arsenault, 2003; Lander, 2006; O'Brien et al., 2006; Dyke, 2008; Koper & Manseau, 2009). These are conifer dominated habitats (>60 yrs old) that generally are not selected by other prey species because they lack sufficient quality and quantity of browse, and therefore typically have lower associated predation risk. Caribou tend to avoid early-succession hardwood-dominated covertypes with high quantities of regenerating browse that are preferred by other prey species and have a higher associated predation risk. However, anthropogenic disturbances tend to occur in mature and old-growth upland forest habitat, including those adjacent to treed peatlands. This has the effect of increasing the population density of other prey species as well as predator numbers and predator access efficiency, which compromises the

functional value of treed peatlands and upland jackpine as refuges from excessive predation by increasing caribou-wolf encounter rates (mortality risk) (James, 1999; James et al. 2004). Messier (1995a) calculated a minimum density of 0.20 moose/km² as required to support a wolf population. The long-term mean (1979-2006) winter moose population density for the PAGE area was 0.15/km², with a low of 0.08/km² in 2005 (Arsenault, 2000; Arsenault, unpubl. data). Winter elk population densities tend to average about 0.28/km² in core range, with herds occurring in a clumped distribution along the forest fringe at the southern boundary of the PAGE area and PANP, in regenerating cut-overs in the Clark Lakes area northwest of the Park, and in the Montreal Lake area along the east side of the Park (Arsenault, 2008; Arsenault, unpublished data). White-tailed deer tend to concentrate in highest densities $(2.10 - 2.80/\text{km}^2)$ along the forest fringe and occur at lower densities (0.69 - 1.40)km²) northward in suitable habitat (which is limited) with an overall long-term (1984-2003) mean density of 1.18/km² for the PAGE area (Arsenault, 2005). Mule deer occur within the PAGE area, but in very low densities and in a sporadic occurrence (Arsenault, 2005). Prior to calving, pregnant female caribou disperse from conspecifics to minimize predation risk to their newborn calf. The associated loss of habitat connectivity has the potential to limit the ability for caribou to disperse to safer refuges from predators.

Conservation of boreal woodland caribou requires land management strategies that not only maintain caribou habitat within the landscape mosaic, but also maintains a landscape pattern and structure that ensures structural and functional connectivity among habitats to facilitate movement of caribou throughout the landscape. Henein & Meriam (1990) found that corridors connecting habitat patches influences metapopulation dynamics and persistence based on corridor quality but not quantity. They concluded that meta-populations with habitat patches connected by high quality corridors have a larger population at equilibrium than those connected by >1 low quality corridors and that addition of a habitat patch connected by low quality corridors has a negative effect on overall meta-population size. They also concluded that meta-populations in isolated patches connected by low quality corridors were the most vulnerable to local extinction, but any connection between isolated patches was better than no connection with respect to persistence and population size at equilibrium. The degree to which the intervening landscape between habitat patches facilitates or impedes movement corresponds to the connectivity of the landscape (Taylor et al., 1993; O'Brien et al. 2006; Fall et al., 2007, Galpern et al., 2010). Landscape connectivity influences the ability for caribou to access habitat, avoid predators, move between core portions of their range and between ranges, and contribute to gene flow (Manseau *et al.*, 2008).

The conclusion reached from the PAGE vegetation analysis is that 50 years ago the forest was younger, presenting less, and widely distributed older coniferous stands across the landscape (Arlt & Manseau, 2011). Their results suggest an aging landscape in the present, with a larger amount of old coniferous stands attributed to changes in fire incidence and fire management strategies. But the functional value of the older forest is likely reduced by its proximity to roads, cut blocks and hardwood-mixedwood forest stands (Arlt & Manseau, 2011). The fur harvest data for bears and wolves is inadequate to assess predator population trend in the PAGE because the data lacks information on trapper effort. Licensed harvest of moose and elk in the PAGE area has remained relatively stable from the mid 1980s through mid 2000s (Arsenault, 2000; Arsenault, 2005; Arsenault, 2008). However, the licensed harvest of white-tailed deer increased by almost 200% over the same period, particularly near the southern portions of the PAGE along the forest fringe (Arsenault, unpubl. data).

The effects of diminished habitat connectivity of the PAGE for caribou are potentially manifested through:

- 1. Direct habitat loss from landscape disturbances.
- 2. Functional habitat loss because of displacement, avoidance and barrier effects of disturbances and anthropogenic features.
- 3. Alteration of predator-prey dynamics as a consequence of increases in other cervid species attracted to recent cut-overs and burns, which supports a larger predator base.
- 4. Increased mortality risk to caribou because of increased predator densities, ease of predator access and search efficiency to habitat patches proximate to local caribou populations because of the extensive road/trail network.
- 5. Fragmentation of the PAGE caribou into small, sedentary, highly clustered local populations with limited movement among habitat patches throughout the landscape. Effective habitat connectivity is critical for the long-term persistence of caribou.

Recommended land management strategies

The data used to develop the following land management strategies are by no means perfect, resulting in landscape planning and management within an environment of uncertainty. In some situations the recommended strategies would apply to local population ranges (including specific habitat types) and in others they would apply at a broader scale (WCMU and beyond). Regardless, application of the strategies should be conducted within an adaptive management framework accompanied by ecological performance measures for monitoring and assessing their effectiveness against established targets and objectives.

Declines in caribou populations and range occupancy are likely to continue in the PAGE area because of the high degree of habitat fragmentation, loss of habitat connectivity, alteration of adjacent forest stands leading to increased numbers of other prey species, and associated increased predation risk. Wolf density for the PAGE area based on a linear regression model using the relationship of wolf density and ungulate biomass (per Keith, 1983; Messier, 1995b; Mech & Boitani, 2003), yields a density of 0.01-0.02 wolves/km². Urton (2004) estimated the wolf density in the PAGE area to be about 0.02/km². There are inadequate data to estimate bear populations for the PAGE area.

Landscapes with fragmented caribou populations or clustered distributions require spatially targeted action to protect and manage for preferred habitat (including movement corridors). A common resolution to problems associated with human disturbance impacts on the landscape is to separate human activities from centers of sensitive wildlife activity by use of buffer zones or set-back distances within which human activity is restricted to minimize impacts (Arsenault, 2009). Refugia from human encroachment and landscape disturbance may be vital to retaining range occupancy of PAGE caribou (Schaeffer, 2003; Vors et al., 2007). Effective protection may be possible through establishment of protected areas, landscape planning and management of the amount and type of human developments and natural disturbances to ensure ecological functionality of the boreal landscape. Natural disturbances are integral to molding the structure and function of landscapes, ecosystems and species (Landres et al., 1999; Saskatchewan Ministry of Environment, 2009). Natural variability is defined as spatial and temporal variation in the ecological conditions that are relatively unaffected by humans within a defined geographical area and period of time appropriate to an expressed goal (Landres et al., 1999, Oliver et al., 2007). Failure to consider the occurrence and biological fitness of boreal caribou could result in incorrect assessments of critical habitat importance and ecological integrity to disturbance-generated landscape mosaics, leading to ineffective land management strategies influencing set-back distances or attempts by industry at natural

disturbance emulation (Landres *et al.*, 1999; Laliberte and Ripple, 2004; Arsenault, 2009). Caribou conservation requires land management strategies that maintain caribou habitat, favor habitat connectivity, and supports sustainable caribou populations (O'Brien *et al.*, 2006).

The following land management strategies are recommended as a contribution to the conservation of boreal caribou populations and range over the long term in the Boreal Plain Ecosystem:

- 1. Retain large softwood (black spruce, jackpine, larch tamarack) habitat patches (>60 yrs old), and a large proportion of mature and old growth forest interior within local population ranges. Caribou are at greater predation risk if they have a relatively small proportion of mature and old forest in their individual home ranges and the collective local population range (Wittmer *et al.*, 2007). Larger habitat patches that support larger local populations present a better opportunity to ensure long-term population viability than do small patches with small, highly fragmented, local populations (Barryman, 2002; Baguette & Stevens, 2003).
- 2. Habitat selection (e.g. calving site) occurs at multiple spatial scales, therefore in highly fragmented landscapes it is important to maintain buffer habitat (e.g. lichen-rich conifer stands >60 yrs old) surrounding important habitat patches (e.g. important peatland complexes) and sensitive areas to discourage increases of other prey species in response to landscape alterations, thus minimizing predation risk. Old growth forest associated with treed peatlands within local population ranges that have been significantly impacted by forest harvesting should be highest priority for extended rotation and wildfire suppression. At low population densities, caribou have lower survival probabilities in areas with greater amounts of young hardwood and mixedwood forest (Wittmer et al., 2007). Therefore, the spatial pattern of buffering habitat patches along the margins of preferred caribou habitat within and among local caribou population ranges is important to consider when anthropogenic disturbance is proposed.
- 3. Protect habitat selected for the calving period, particularly treed peatlands within local population ranges, to increase likelihood of calf survival and aid in recovery. There should be no access development or peat and forest harvesting in important peatlands or treed peatland complexes within local population ranges such as those in the Montreal Lake portion of the PAGE area.

- 4. Identify, prioritize, and protect high quality habitat and movement corridors linking habitat patches and clusters using telemetry data and habitat structural connectivity analysis (O'Brien et al., 2006; Fall et al., 2007) to ensure a landscape mosaic that is functional for caribou. Prioritization of corridors for protection and/or restoration should consider caribou distribution. local population range occupancy, movement patterns, size of available corridors, disturbance magnitude, and population viability. Caribou habitat is characterized as high-quality habitat patches embedded within a matrix that facilitates foraging, predator avoidance and protection from human disturbances (Rettie & Messier, 2000; Smith et al., 2000; James et al., 2004; O'Brien et al., 2006). The least-cost paths connecting core habitat clusters can point to movement corridors (Taylor et al., 1993; O'Brien et al., 2006). Landscape conservation and restoration goals should concentrate effort on maintaining high quality linkages between clusters of habitat patches within and among local populations, and ensure that the required connectivity is effectively buffered from anthropogenic disturbance. The connectivity between the remnant habitat patches within and among local populations is essential to animal movement, dispersal ability, gene flow, and ultimately the long-term persistence of local populations, particularly if the WCMU population is small and/or exists at low density (Arsenault, 2003). Recolonization of abandoned habitat is critical for regional survival of fragmented populations (Fahrig & Merriam, 2002). Contiguous habitat promotes more movement of species and links among local populations than fragmented habitat. The greater the distance between ranges, the larger the width of corridor required to facilitate movement between local populations or regional populations.
- 5. Fire salvage should not occur in or adjacent to treed peatlands or peatland complexes within local caribou population ranges. This will help to minimize creation of, or improve, access for predators, to minimize disturbance of impacted habitat, and to avoid creation of movement barriers. This is an important consideration for the Bittern Lake portion of the PAGE area.
- 6. Ecosystem-level disturbance such as developments and resource extraction activities should be planned in a way to minimize habitat fragmentation and/or avoid creation of barriers to movement within and among critical habitats. The scientific literature documents displace-

ment of caribou from anthropogenic disturbance as far as 1000 m to 1200 m depending on the type, duration, extent, frequency and magnitude (Smith *et al.*, 2000; Dyer *et al.*, 2001). Therefore, identification of critical habitat should occur at the local population scale within each WCMU to ensure it is well distributed and connected at the local population scale and at the WCMU scale. This would ensure the long-term persistence of caribou within each WCMU. It is also important to ensure that industry activity set-back distances are sufficient to effectively buffer local caribou populations and sensitive locations from the disturbance.

- 7. Forest planning and harvest operations within and among local caribou population ranges should ensure that caribou are able to freely move across the forest landscape through time. For example, if caribou habitat is to be logged, it is better to log a few larger patches that more closely emulate the pattern of wildfire. This strategy should minimize the response of other prey species populations to increase, and result in a cut-block that more closely resembles lichen-rich caribou habitat once the cut-block has matured into older aged stands (>60 years old), minimize access development that might improve predator efficiency, and retain higher quality caribou movement corridors through reduced edge effects and fragmentation that would result from multiple smaller cut-blocks.
- 8. Minimize disturbance around sensitive caribou habitat by concentrating disturbances spatially and temporally. This will help minimize the cumulative effects of disturbance in occupied caribou range. Constraints on anthropogenic disturbance should depend on the level of natural disturbance, degree of connectivity within and among core use areas, population viability, and factors limiting to caribou in the planning area. This is an important consideration in the Clarke Lakes portion of the PAGE area which has been significantly impacted by forest harvesting.
- Landscape planning should occur at a WCMU (or comparable) scale over a natural fire cycle. The historical fire cycle for the Boreal Plain Ecozone in Saskatchewan is estimated at 50 – 150 years (Weir *et al.*, 2000; Li *et al.*, 2005; Saskatchewan Ministry of Environment, 2009).
- 10. Manage fire suppression, forest harvesting and silviculture activities to emulate an appropriate natural disturbance regime that will mimic natural forest patterns to the greatest extent possible for forest habitat renewal. Saskatchewan Ministry

of Environment (2009) has developed draft natural forest pattern standards and guidelines for the forest industry intended to produce landscapes and harvest areas that look and function like landscapes and disturbance patches created by natural disturbances such as fire.

- 11. Use reclamation prescriptions and silviculture practices within impacted local population ranges that encourage rapid re-establishment of caribou habitat. Such prescriptions and practices will act by decreasing shrub response and early successional hardwoods, and speeding succession to a structural stage preferred by caribou. This should be applied to the Clarke Lakes area and cut-over areas along the north side of PANP.
- 12. Access management for all industries should include reclaiming seasonal roads and trails that are no longer needed, through reforestation, as well as access restrictions and limitations on new access development in proximity (within 1 km) to high quality caribou habitat and movement corridors within and among local population ranges throughout the PAGE area and larger SW-WCMU. This would aid in reducing human disturbance, predation risk, functional habitat loss through displacement caused by disturbance, potential barriers to movement, intrusiveness of the linear feature, as well as limiting further landscape fragmentation.
- 13. Access planning should occur at large spatial (WCMU scale) and broad temporal scales with development focused on shared use. This will help to minimize excessive or unnecessary access development and reclamation when no longer required. Roads should avoid high caribou use areas and clusters of selected habitat types such as jackpine and treed peatland complexes. Use of winter roads in caribou habitat is desirable. because of their short duration of use and minimal footprint. The short-term disturbance during a winter season is preferable to the long-term effect of a permanent road. Predator efficiency is reduced by limiting their line of sight to less than 200m, which is further supported by ungulate selective use of forest openings to forage within 100-200 m of cover (Hamilton & Drysdale, 1975; Rost & Bailey, 1979; Thomas et al., 1979; Dunford et al., 2003; Arsenault, 2009). Linear developments should ensure reduced line-of-sight (<200 m) where it occurs within local population ranges to provide adequate visual and winter escape cover (wildlife blinds), reduce predation risk by minimizing line-of-sight for predators, to and mitigate potential barriers for movement.

- 14. Within local population ranges, maintain appropriate community dynamics, species interactions and functional diversity such as spatial separation from other cervid species and predators. Mortality risk to PAGE caribou from predation could be reduced in areas requiring habitat restoration by aggressively hunting other prey to impede predator numbers, and concurrently allowing post-disturbance vegetative recovery to a state less favorable to other prey species.
- 15. Periodically monitor genetic status within and among WCMU populations. This will help to provide early assessment of impacts on ecological integrity from the cumulative effects of anthropogenic and natural disturbance, vegetation change, and landscape restoration efforts.
- 16. Quantify the current level of human disturbance within a WCMU and use this to stratify into high, medium and low levels to determine risk, to prioritize areas of management concern, and to plan for suitable future caribou habitat.
- 17. Assess WCMUs in relation to development thresholds. This could include quantifying landscape level development impact thresholds such as linear corridor densities, effective set-back distances to buffer core caribou habitats from various disturbance types, and effective habitat connectivity levels that support caribou range occupancy.

Acknowledgements

This research was funded through grant awards provided by Prince Albert National Park, Parks Canada Species at Risk Recovery Action and Education Fund, Parks Canada Ecological Integrity Innovation and Leadership Fund, Saskatchewan Environment, Saskatchewan Fish and Wildlife Development Fund, Weyerhaeuser Canada Inc., and Prince Albert Model Forest. Contributions in-kind were provided through a collaborative research partnership between the Western and Northern Service Centre of Parks Canada, Prince Albert National Park, Saskatchewan Environment, University of Manitoba Natural Resources Institute, Prince Albert Grand Council, Weyerhaeuser Canada Ltd. and the National Resources DNA Profiling and Forensic Centre at Trent University. We thank the members of our core team (Tim Trottier, Dan Frandsen, Fiona Moreland, Ed Beveridge, Brad Tokaruk, Ed Kowal, Rhys Beaulieau, Brian Christensen, Ryan Kay, Richard Pither), graduate students (Maria Arlt, Mark Ball, Casidhe Dyke, Peter Hettinga), and research assistants (Sonesinh Keobouasone, Jennifer Keeney, Lois Koback) as well as the numerous individuals who assisted with various data collection activities for this study.

We thank Bob Wynes, Tim Trottier and Ed Kowal for providing comments on the manuscript.

References

- Acton, D.F., Padbury, G.A., & Stushnoff, C.T. 1998. The ecoregions of Saskatchewan. Canadian Plains Research Center, University of Regina. 205pp.
- Adams, L.G., Singer, F.J., & Dale, B.W. 1995. Caribou calf mortality in Denali National Park, Alaska. J. Wildl. Manage. 59(3):584-594.
- Akcakaya, H.R. 2001. Linking population-level risk assessment with landscape and habitat models. – *The Sci*ence of the Total Environment 274:283-291.
- Arlt, M.L. 2009. Historical distribution of boreal caribou (*Rangifer tarandus caribou*) in the Prince Albert Greater Ecosystem. M.Sc. Thesis. Univ. of Manitoba, Winnipeg, Manitoba. 107pp.
- Arlt, M.L. & Manseau, M. 2011. Changes in caribou distribution and land cover in and around Prince Albert National Park: different management strategies, different landscapes. – *Rangifer* Special Issue No. 19.
- Arsenault, A.A. 2000. Status and management of moose (*Alces alces*) in Saskatchewan. Saskatchewan Environment and Resource Management. Fish and Wildlife Tech. Rep. 00-1. 84pp.
- Arsenault, A.A. 2003. Status and conservation management framework for woodland caribou (*Rangifer taran-dus caribou*) in Saskatchewan. Saskatchewan Environment. Fish and Wildlife Tech. Rep. 2003-03. 40pp.
- Arsenault, A.A. 2005. Status and management of wildlife in Saskatchewan, 2002 and 2003. Saskatchewan Environment. Resource Technical Report 2005-02. 89pp.
- Arsenault, A.A. 2008. Saskatchewan elk (*Cervus elaphus*) management plan – update. Saskatchewan Ministry of Environment. Fish and Wildlife Tech. Rep. 2008-02). 63pp.
- Arsenault, A.A. 2009. Disturbance impact thresholds: recommended land use guidelines for protection of vertebrate species of concern in Saskatchewan. Saskatchewan Ministry of Environment. Lands Branch – Fish and Wildlife Branch Technical Report 2009-06. 94pp.
- Baguette, M. & Stevens, V.M. 2003. Local populations and metapopulations are both natural and operational categories. – *Oikos* 101:661-663.
- Ball, M.C. 2008. Conservation genetics of Canadian boreal caribou (*Rangifer tarandus caribou*). PhD Thesis, Trent University, Peterborough, Ontario. 222pp.
- Ball, M.C., Pither, R., Manseau, M., Clark, J., Petersen, S.D., Kingston, S., Morrill, N., & Wilson, P. 2006. Characterization of target nuclear DNA from faeces reduces technical issues associated with the assumptions of low-quality and quantity template. – *Conserv. Genetics* 8:577-586.
- Ball, M.C., Manseau, M., & Wilson, P. 2010. Integrating multiple analytical approaches to spatially delineate and characterize genetic population structure: an application to boreal caribou in central Canada. – *Conserv. Genetics* 11(6):2131-2143.

- Bergerud, A.T. 1992. Rareness as an anti-predator strategy to reduce predation risk for moose and caribou. – In: McCullough, D.R. & Barrett, R.B. (eds.). Wildlife 2001: Population. Elsevier, London, pp. 1008-1021.
- Bergerud, A.T., Butler, H.E., & Miller, D.R. 1984. Antipredator tactics of calving caribou: dispersion in mountains. – *Can. J. Zool.* 62:1566-1575.
- Berryman, A.A. 2002. Population: a central concept for ecology? – Oikos 97:439-442.
- Bradshaw, C.J.A., Hebert, D.M., Rippin, A.B., & Boutin, S. 1995. Winter peatland habitat selection by woodland caribou in northeastern Alberta. – Can. J. Zool. 73:1567-1574.
- Bradshaw, C.J.A., Boutin, S., & Hebert, D.M. 1998. Energetic implications of disturbance caused by petroleum exploration to woodland caribou. – Can. J. Zool. 76: 1319-1324.
- Brown, G.S., Rettie, J.W., Brooks, R.J., & Mallory, F.F. 2007. Predicting the impacts of forest management on woodland caribou habitat suitability in black spruce boreal forest. – *Forest Ecol. and Manage*. 245:137-147.
- Brown, K.G., Elliot, C., & Messier, F. 2000a. Seasonal distribution and population parameters of woodland caribou in central Manitoba: implications for forestry practices. – *Rangifer* Special Issue No. 12:85-94.
- Brown, W.K., Rettie, W.J., Wynes, B, & Morton, K. 2000b. Wetland habitat selection by woodland caribou as characterized using the Alberta Wetland Inventory. *– Rangifer* Special Issue No. 12:153-157.
- Burles, D.W., Whaley, K.R., Wilson, E.B., & Ferguson, L.E. 1978. Aerial caribou survey, Prince Albert National Park. Parks Canada, Dept. Ind. and Nor. Affairs. 19pp.
- Camus, P.A. & Lima, M. 2002. Populations, metapopulations, and the open-closed dilemma: the conflict between operational and natural population units. – *Oikos* 97:433-438.
- Côté, S.D., Dallas, J.F., Marshall, F., Irvine, R.J., Langvatn, R., & Albon, S.D. 2002. Microsatellite DNA evidence for genetic drift and philopatry in Svalbard reindeer. – *Molecular Ecology* 11(10):1923-1930.
- Cundiff, B. & Gray, T. 2004. Grey ghosts: can we save woodland caribou in Canada's boreal forest? Canadian Parks and Wilderness Society. Ottawa, Ontario.
- Cronin, M.A. 2003. Research on deer taxonomy and its relevance to management. – *Ecoscience* 10(4):432-442.
- PAGC (Prince Albert Grand Council). 2002. Woodland caribou Habitat Stewardship Program project. 131pp.
- Dunford, J., Nolan, J.W., & McLoughlin, P.D. (eds). 2003. Boreal Caribou Research Program 2003 Research Summary. 57pp.
- Dussault, C, Ouellet, J.-P., Courtois, R., Huot, J., Breton, L., & Jolicoeur, H. 2005. Linking moose habitat selection to limiting factors. – *Ecography* 28:619-628.
- Dyer, S.J., O'Neill, P.O., Wasel, S.M., & Boutin, S. 2001. Avoidance of industrial development by woodland caribou. – J. Wildl. Manage. 65:531-542.

- Dyer, S.J., O'Neill, P.O., Wasel, S.M., & Boutin, S. 2002. Quantifying barrier effects of roads and seismic lines on movement of female woodland caribou in northeastern Alberta. – *Can. J. of Zool.* 80:839-845.
- Dyke, C. 2008. Characterization of woodland caribou (Rangifer tarandus caribou) calving habitat in the boreal plains and boreal shield ecozones of Manitoba and Saskatchewan. M. N. R. M. Thesis. University of Manitoba, Winnipeg, Manitoba. 96pp.
- Edmunds, E.J. 1988. Population status, distribution, and movements of woodland caribou in west central Alberta. – Can. J. Zool. 66:817-826.
- Environment Canada. 2007. Recovery strategy for the Woodland Caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada (Draft), June 2007. Species at Risk Act Recovery Strategy Series. Ottawa: Environment Canada. v + 48pp.
- Environment Canada. 2008. Scientific review for the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada. August 2008. Environment Canada. Ottawa. 238pp.
- Fall, A. & Fall, J. 2001. A domain-specific language for models of landscape dynamics. – *Ecological Modeling* 141:1-18.
- Fall, A., Fortin, M-J., Manseau, M., & O'Brien, D. 2007. Spatial graphs: principles and applications for habitat connectivity. – *Ecosystems* 43:123-137.
- Fahrig, L. & Merriam, G. 2002. Conservation of fragmented populations. - Conserv. Biol. 8(1):50-59.
- Ferguson, S.H., Bergerud, A.T., & Ferguson, R. 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. – *Oecologia* 76:236-245.
- Forman, R.T.T. 1995. Land Mosaics: the Ecology of Landscapes and Regions. Cambridge University Press, New York.
- Frid, A. & Dill, L. 2002. Human-caused disturbance stimuli as a form of predation risk. – *Conserv. Ecology* 6(1):11. [online] URL: http://www.consecol.org/vol6/ iss1/art11.
- Fuller, T.K. & Keith, L.B. 1981. Woodland caribou population dynamics in northeastern Alberta. – J. Wildl. Manage. 45(1):197-213.
- Galpern, P., Manseau, M., & Fall, A. 2010. Patch-based graphs of landscape connectivity: A guide to construction, analysis and application for conservation. – *Biol. Conserv.* [online]. doi:10.1016/j.biocon.2010.09.002
- Godkin, G.F. 1986. Fertility and twinning in Canadian reindeer. *Rangifer* Special Issue No. 1:145-150.
- Government of Saskatchewan. 2009. A guide to the environmental assessment process. [online] URL: http://www.environment.gov.sk.ca/Default. aspx?DN=51580b36-1575-4460-a9c8-2a3bf825ae9a.
- Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P., & Heard, D.C. 2006. Calf survival of woodland caribou in a multi-predator ecosystem. – Wildl. Monogr. 165:1-32.

- Hamilton, G.D. & Drysdale, P.D. 1975. Effects of cut-over width on browse utilization by moose. Proc 11th N. Amer. Moose Conf. Workshop 11:1-12.
- Henein, K. & Merriam, G. 1990. The elements of connectivity where corridor quality is variable. – Landscape Ecol. 4(2/3):157-170.
- Hettinga, P. N., Manseau, M., Arnason, N., Cross, D., Whaley, K., & Wilson, P. 2010. Estimating the size and trend of the North Interlake woodland caribou (*Rangifer tarandus caribou*) population using fecal DNA and capture-recapture models. – J. Wildl. Manage. (submitted).
- Hirai, T. 1998. An evaluation of woodland caribou calving habitat in the Wabowden area, Manitoba. M. N. R. M. Thesis, University of Manitoba, Winnipeg, Manitoba.
- Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. – *Ecol. Monogr.* 62:447-502.
- James, A.R.C. 1999. Effects of industrial development on the predator-prey relationship between wolves and caribou in northeastern Alberta. Ph.D. Thesis, University of Alberta, Edmonton, Alberta.
- James, A.R.C. & Stuart-Smith, A.K. 2000. Distribution of caribou and wolves in relation to linear corridors. - J. Wildl. Manage. 64:154-159.
- James, A.R.C., Boutin, S., Hebert, D.M., & Rippin, A.B. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. – J. Wildl. Manage. 68:799-809.
- Johnson, C.J., Alexander, N.D., Wheate, R.D., & Parker, K.L. 2003. Characterizing woodland caribou habitat in sub-boreal and boreal forests. – *Forest Ecol. and Manage*. 180:241-248.
- Johnson, C.J., Seip, D.R., & Boyce, M.S. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple scales. – J. Appl. Ecol. 41:238-251.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. - *Ecology* 61:65-71.
- Keith, L.B. 1983. Population dynamics of wolves. In: L.N. Carbyn (ed.). Wolves in Canada and Alaska: their status, biology, and management. Can. Wildl. Serv. Rep. Ser. No. 45, pp. 66-77.
- Koper, N. & Manseau, M. 2009. Generalized estimating equations and generalized linear mixed-effects models for modeling resource selection. – J. Animal Ecol. 46:590-599.
- Lacy, R.C. 1997. Importance of genetic variation to the viability of mammalian populations. – J. Mammalogy 78:320-335.
- Laliberte, A.S. & Ripple, W.J. 2004. Range contractions of North American carnivores and ungulates. – *Bioscience* 54(2):123-138.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455-1460.

- Lande, R. 2002. Incorporating stochasticity in population viability analysis. – *In*: Beissinger, S.R.& McCullough, D.R. (eds.). *Population Viability Analysis*. Univ. of Chicago Press, Chicago, pp. 18-40.
- Lander, C.A. 2006. Distribution and movements of woodland caribou on disturbed landscapes in west-central Manitoba: implications for forestry. M. N. R.M. Thesis. University of Manitoba, Winnipeg, Manitoba. 119pp.
- Landres, P.B., Morgan, P., & Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. – *Ecol. Appl.* 9(4):1179-1188.
- Lantin, E., Drapeau, P., Pare, M., & Bergeron, Y. 2003. Preliminary assessment of habitat characteristics of woodland caribou calving areas in the Claybelt region of Quebec and Ontario, Canada. – *Rangifer Special Issue* No. 14:247-254.
- Lavigueur, L. & Barrette, C. 1992. Suckling, weaning, and growth in captive woodland caribou. – Can. J. Zool. 70:1753-1766.
- Li, C., Barclay, H., Liu, S., & Campbell, D. 2005. Simulation of historical and current fire regimes in central Saskatchewan. – For. Ecol. Manage. 208 (1):319-327.
- Loew, S.S. 2000. Role of genetics in conservation biology. – In: Ferson, S. & Burgman, M. (eds.). Quantitative Methods for Conservation Biology. Springer-Verlag Inc., New York, pp. 226-258.
- Mahoney, S.P. & Virgil, J.A. 2003. Habitat selection and demography of a non-migratory woodland caribou population in Newfoundland. – *Can. J. Zool.* 81:321-334.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., & Erickson, W.P. 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. 2nd Ed. Chapman & Hall. 221pp.
- Manseau, M, Fall, A., O'Brien, D., & Fortin, M.-J. 2002. National parks and the protection of woodland caribou: a multi-scale landscape analysis method. – *Re-search Links* 10(2):24-28.
- Manseau, M., Ball, M., Wilson, P., & Fall, A. 2008. Relationship between landscape connectivity and gene flow for boreal caribou: clues for conservation. Presentation at the12th North American Caribou Workshop, Labrador, Canada.
- Mayr, E. 1963. *Populations, Species, and Evolution*. Harvard University Press, Cambridge, Massachusetts.
- McDonald, J.E. & Martell, A.M. 1981. Twinning and post-partum activity in barren-ground caribou. *Can. Field Nat.* 95(3):354-355.
- McLoughlin, P.D., Dzus, E., Wynes, B., & Boutin, S. 2003. Declines in populations of woodland caribou. -J. Wildl. Manage. 67(4):755-761.
- McLoughlin, P.D., Paetkau, D., Duda, M, & Boutin, S. 2004. Genetic diversity and relatedness of boreal caribou populations in western Canada. – *Biol. Conserv.* 118:593-598.

- Mech, L.D. & Peterson, R.O. 2003. Wolf-prey relations. – In: L.D. Mech & L. Boitani (eds.). Wolves: Behavior, Ecology, and Conservation. Univ. of Chicago Press, p. 148.
- Messier, F. 1995a. Social organization, spatial distribution, and population density of wolves in relation to moose density. – *Can. J. Zool.* 63:1068-1077.
- Messier, F. 1995b. On the functional and numerical responses of wolves to changing prey density. In: L.N. Carbyn, S.H. Fritts, & D.R. Seip, (eds.). Ecology and Conservation of Wolves in a Changing World. Proc 2nd N. Amer. Symposium on Wolves, Edmonton, Canada. Can. Circumpolar Institute. Occ. Publ. Ser. No. 35, pp. 187-198.
- Mitchell, S.C. 2005. How useful is the concept of habitat? - a critique. - 0*ikos* 110(3):634-638.
- Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O., & Newton, A. 2003. Progressive impact of piecemeal infrastructure on wild reindeer. – *Biol. Conserv.* 113:307-317.
- O'Brien, D., Manseau, M., Fall, A., & Fortin, M.-J. 2006. Testing the importance of spatial configuration of winter habitat for woodland caribou: an application of graph theory. – *Biol. Conserv.* 130(1): 70-83.
- Oliver, I., Jones, H., & Schmoldt, D.L. 2007. Expert panel assessment of attributes for natural variability benchmarks for biodiversity. – *Austral Ecol.* 32:453-475.
- Orians, G.H. & Wittenberger, J.F. 1991. Spatial and temporal scales in habitat selection. – Amer. Nat. 137 (Supplement):S29-S49.
- Post, E., Boving, P.S., Pedersen, C., & MacArthur, M.A. 2003. Synchrony between caribou calving and plant phenology in depredated and non-depredated populations. – *Can. J. Zool.* 81:1709-1714.
- Racey, G. & Arsenault, A.A. 2007. In search of a critical habitat concept for woodland caribou, boreal population. – *Rangifer* Special Issue No. 17:29 – 37.
- Ray, C. 2001. Maintaining genetic diversity despite local extinctions: effects of population scale. – *Biol. Conserv.* 100:3–14.
- Reed, M.J., Doerr, P.D., & Walters, J.R. 1986. Determining minimum population sizes for birds and mammals. – Wildl. Soc. Bull. 14:255-261.
- Rettie, W.J. 1998. The ecology of woodland caribou in central Saskatchewan. PhD Thesis. Department of Biology. University of Saskatchewan. Saskatoon, Saskatchewan. 179pp.
- Rettie, J.W. & Messier, F. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. – *Can. J. Zool.* 76:251-259.
- Rettie, J.W., & Messier, F. 2000. Range use and movement rates of woodland caribou in Saskatchewan. – *Can. J. Zool.* 79:1933-1940.
- Rettie, J.W. & Messier, F. 2001. Range use and movement rates of woodland caribou in Saskatchewan. – Can. J. Zool. 79:1933-1940.

- Rock, T.W. 1992. A proposal for the management of woodland caribou in Saskatchewan. Saskatchewan Natural Resources. Wildlife Branch Tech. Rep 92-3. 28pp.
- Rutberg, A.T. 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. – Amer. Nat. 130:692-710.
- Saskatchewan Environment. 2007. Recovery strategy for boreal woodland caribou (Rangifer tarandus caribou) in Saskatchewan. Saskatchewan Environment. Fish and Wildl. Tech. Rep. 2007-draft. 46pp.
- Saskatchewan Ministry of Environment. 2009. Natural forest pattern standards and guidelines for the Saskatchewan provincial forest. Draft 12, Feb 2009, Saskatchewan Environment, Forest Service Branch. 23pp.
- Schaeffer, J.A. 2003. Long-term range recession and the persistence of caribou in the taiga. – *Conserv. Biol.* 17(5):1435-1439.
- Schaefer, J.A. 2006. Towards maturation of the population concept. – Oikos 112: 236-240.
- Schaefer, J.A., Bergman, C.M., & Luttich, S.N. 2000. Site fidelity of female caribou at multiple scales. – Landscape Ecology 15:731-739.
- Schaefer, J.A. & Mahoney, S.P. 2007. Effects of progressive clearcut logging on Newfoundland caribou. – J. Wildl. Manage. 71(6):1753-1757.
- Schaefer, J.A. & W.O. Pruitt, Jr. 1991. Fire and woodland caribou in southeastern Manitoba. – Wildl. Monogr. 116:1-39.
- Schindler, D.W., Walker, D., Davis, T., & Westwood, R. 2007. Determining the effects of an all weather logging road on winter woodland caribou habitat use in south-eastern Manitoba. – *Rangifer* Special Issue No. 17:209-217.
- Schneider, R.R., Wynes, B., Wasle, S., Dzus, E., & Hiltz, M. 2000. Habitat use by caribou in northern Alberta, Canada. – *Rangifer* 20:43-50.
- Seip, D.R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. – Can. J. Zool. 70: 1494-1503.
- Shaffer, M.L. 1981. Minimum population sizes for species conservation. – *BioScience* 31:131-134.
- SKCDC (Saskatchewan Conservation Data Center). 2003. Saskatchewan activity restriction guidelines for sensitive species in natural habitats. [online] URL: http://www. biodiversity.sk.ca/Docs/SKactivityrestrictions.pdf.
- Smith, K.G., Ficht, E.J., Hobson, D., Sorensen, T.C., & Hervieux, D. 2000. Winter distribution of woodland caribou in relation to clear-cut logging in west-central Alberta. – *Can. J. Zool.* 78:1493-1440.
- Soper, J.D. 1951. The mammals of Prince Albert National Park, Saskatchewan, Canada. Dept. Res. and Dev., Dev. Ser. Br., Can. Wildl. Serv. Ser. 1 No. 5. 54pp.
- Sorensen, T., McLoughlin, P.D., Hervieux, D., Dzus, E, Nolan, J., Wynes, B., & Boutin, S. 2008. Deter-

mining sustainable levels of cumulative effects for boreal caribou. – J. Wildl. Manage. 72(4):900-905.

- SMEGAC (Saskatchewan Mineral Exploration and Government Advisory Committee). 2007. Mineral exploration guidelines for Saskatchewan. [online] URL: http://www. environment.gov.sk.ca/Default.aspx?DN=52a8a117-332f-4c49-89b9-2f90d79bca5a.
- Steen, H. & Haydon, D. 2000. Can population growth rates vary with the spatial scale at which they are measured? – J. Anim. Ecol. 69:659-671.
- Taylor, P.D., Fahrig, L, Henein, K., & Merriam, G. 1993. Connectivity is a vital element of landscape structure. – Oikos 68:571-572.
- Thomas, C. & Kunin, W.E. 1999. The spatial structure of populations. – J. Anim. Ecol. 68:647-657.
- Thomas, D.C., & Gray, D.R. 2002. Update COSEWIC status report on the woodland caribou *Rangifer tarandus caribou* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. 1-98pp.
- Thomas, J.W., Black Jr., H., Scherzinger, R.J., & Pedersen, R.J. 1979. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA Forest Service, Agricultural Handbook No. 553.
- Tilman, D., May, R.M., Lehman. C.L, & Nowak, M.A. 1994. Habitat destruction and the extinction debt. – *Nature* 371:65-66.
- Tischendorf, L., & Fahrig, L. 2000. On the usage and measurement of landscape connectivity. – Oikos 90:7-19.
- Trottier, T.W.P. 1988. A survey of woodland caribou occurrences in Saskatchewan, 1960-1987. Saskatchewan Parks, Recreation and Culture. Wildlife Branch. Wildlife Population Information Base 88-WPM-9. 24pp.
- Urton, E.J.M. 2004. Population genetics, foraging ecology, and trophic relationships of grey wolves in central Saskatchewan. M.Sc. Thesis, Univ. of Saskatchewan. 87pp.
- Vors, L.S., Schaefer, J.A., Pond, B.A., Rodgers, A.R., & Patterson, B.R. 2007. Woodland caribou extirpation and anthropogenic landscape disturbance in Ontario. - J. Wildl. Manage. 71(4):1249-1256).
- Weir, J.M.H, Johnson, E.A., & Miyanishi, K. 2000. Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in western Canada. – *Ecol. Appl.* 10:1162-1177.
- Weir, J.N., Mahoney, S.P., McLaren, B., & Ferguson, S.H. 2007. Effects of mine development on woodland caribou *Rangifer tarandus* distribution. – *Wildl. Biol* 13(1):66-74.
- Wilkinson, C.J.A. 2008. An examination of recovery planning for forest-dwelling woodland caribou (*Rangifer tarandus caribou*) in Ontario, Canada. – *Rangifer* 28(1):13-32.
- Wittmer, H.U.; McLellan, B.N.; Serrouya, R.; & Apps, C.D. 2007. Changes in landscape composition influence the decline of a threatened woodland caribou population. – J. Appl. Ecol. 76:568-579.