

The influences of wolf predation, habitat loss, and human activity on caribou and moose in the Alberta oil sands

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Woodland caribou (*Rangifer tarandus caribou*) and moose (*Alces alces*) populations in the Alberta oil sands region of western Canada are influenced by wolf (*Canis lupus*) predation, habitat degradation and loss, and anthropogenic activities. Trained domestic dogs were used to locate scat from caribou, moose, and wolves during winter surges in petroleum development. Evidence obtained from collected scat was then used to estimate resource selection, measure physiological stress, and provide individual genetic identification for precise mark–recapture abundance estimates of caribou, moose, and wolves. Strong impacts of human activity were indicated by changes in resource selection and in stress and nutrition hormone levels as human-use measures were added to base resource selection models (including ecological variables, provincial highways, and pre-existing linear features with no human activity) for caribou. Wolf predation and resource selection so heavily targeted deer (*Odocoileus virginiana* or *O hemionus*) that wolves appeared drawn away from prime caribou habitat. None of the three examined species showed a significant population change over 4 years. However, caribou population estimates were more than double those of previous approximations for this area. Our findings suggest that modifying landscape-level human-use patterns may be more effective at managing this ecosystem than intentional removal of wolves.

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Woodland caribou (*Rangifer tarandus caribou*) extirpation is predicted over the next 70 years in the western Canadian province of Alberta. The East Side of the Athabasca River (ESAR) caribou herd – whose ranges partially overlap the Alberta oil sands, the second largest known source of petroleum reserves in the world – is predicted to be extirpated in the next three decades (Schneider *et al.* 2010). However, reliable methods to census at-risk woodland caribou herds in Canada's boreal forest were unavailable until now, partly because forest cover prevents accurate visual counts. Cichowski (2010) estimated the ESAR population to be between 90 and 150 caribou in 2009. Caribou population sizes and trajectories in Alberta have been approximated by coupling two data sources: (1) an abundance estimate made from expert opinion circa 2003, and (2) a cumulative measure of population decline estimated from female mortality and calf recruitment through limited radio-telemetry data (McLoughlin 2003; Cichowski 2010). Nevertheless, the purported trends are worrying, adding to the political and environmental pressures on further development in Alberta's oil sands.

Scientists, managers, and resource developers have been searching for feasible methods to curtail the caribou

decline while supporting energy development. Schneider *et al.* (2010) recommended a triage approach for caribou management in Alberta, prioritizing only those caribou herds deemed most likely to persist for management and conservation; the ESAR population is among those identified as least likely to persist. Perhaps most controversial, wolf (*Canis lupus*) removal has been conducted in the range of one Alberta caribou herd and is advocated as the most effective management approach to curtail the caribou decline (Alberta Caribou Committee 2009; Schneider *et al.* 2010), despite potentially serious negative repercussions for the overall ecosystem (eg trophic cascades; Ripple and Beschta 2006; Terborgh and Estes 2010).

It remains uncertain as to exactly why caribou are declining. In this paper, we consider three prominently argued hypotheses in the ESAR: (1) losses in functional caribou habitat due to the large environmental footprint associated with forestry and oil extraction in the oil sands (Dyer *et al.* 2001; Sorensen *et al.* 2008); (2) physiological stresses resulting from intense, widespread levels of human activity (Bradshaw *et al.* 1997); and (3) wolf-inflicted caribou mortality from habitat modifications that have promoted population growth among deer (*Odocoileus virginiana* or *O hemionus*), moose (*Alces alces*), and thus wolves (James and Stuart-Smith 2000; Alberta Caribou Committee 2009; Latham 2009).

To address these hypothesized causes of the caribou decline, we present a novel, non-invasive approach that includes methods to reliably monitor selected large-mammal species within this ecosystem. We used detection dogs to locate the scat of caribou, moose, and wolves across the

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landscape. Scat locations were used to estimate resource selection probability functions (RSPFs; the probability that an animal, post encounter, will use a particular resource, characterized by a combination of environmental variables; Lele and Keim 2006). Collected scat samples were analyzed for genetic capture–mark–recapture (CMR)-based abundance estimates and endocrine-based measures of psychological and nutritional stress.

■ Study area

Located in the Athabasca oil sands south of Fort McMurray, Alberta, between Provincial Highways 63 and 881 (56.0°N, 111.3°W), our study area overlapped two of seven caribou ranges comprising what is identified as the larger caribou herd within the ESAR region. Caribou fidelity to these ranges is high (Stuart-Smith *et al.* 1997). Currently, there is on average greater than 1.5 km of linear features (ie roads, power, pipe, and seismic lines) per square kilometer in the study area. Wildfire is a dominant ecological process; approximately 35% of the study area has been burned during the past 40 years. Human activity across much of the study area is largely confined to winter, when “ice roads” permit vehicular access.

■ Methods

Field sampling and laboratory analyses

Trained domestic dogs were used to detect scat from caribou, moose, and wolves (Wasser *et al.* 2004). The study area was divided into 40 contiguous, 8 km × 8 km cells. One of four dog teams surveyed a different (non-overlapping) ~5-km transect loop within each cell during each of four sampling sessions. Sampling was conducted between mid-December and March 20th of 2006, 2007, and 2009. Sampling routes were predetermined to either maximize the number of different habitat types and anthropogenic disturbances covered (2006) or increase the representation of the most heavily used habitats (subsequent years) to improve sample detection (WebPanel 1). Sampling routes – as well as point locations for each of the 1914 caribou, 1175 moose, and 327 wolf scat samples collected – were recorded by global positioning system technology.

Scat samples were collected for laboratory analysis. Extremely cold temperatures throughout the sampling period resulted in scat being frozen and well-preserved immediately upon defecation. Glucocorticoid (GC) and thyroid hormone metabolite (triiodothyronine, T3) concentrations were assayed from the 2006 fecal samples following Wasser *et al.* (2000, 2004, 2010). GC secretion increases with psychological and nutritional stress (Kitaysky *et al.* 2005), whereas T3 decreases under nutritional stress but remains relatively unchanged in response to psychological stress (Douyon and Scheingart 2002).

We extracted DNA from scat samples using two methods (WebPanel 1): one as described in Wasser *et al.*

(2004) and the other modified from that of Ball *et al.* (2007). Genetic samples from confirmed caribou, moose, and wolf scats were assayed for six species-specific microsatellite loci; in total, 404 caribou, 416 moose, and 74 wolf scat samples were genotyped in 2006, and 726 caribou, 379 moose, and 124 wolf scat samples were genotyped in 2009 (WebTable 1). In 2006, 42%, 86%, and 85% of these samples, respectively, were amplified at enough loci (≥ 3) to be included in CMR analyses (White 2009; WebPanel 1). With improved extraction methods, the amplification success of microsatellite DNA for caribou more than doubled in 2009, increasing the number of samples identified to the individual to 90%, with most samples amplifying at ≥ 5 loci (WebPanel 1).

Evaluating functional habitat loss and resource selection

We used an information criterion to identify RSPF models for caribou and moose from the spatial locations of scat recorded in 2006 and 2007. We first estimated base RSPF models from environmental features, such as terrain complexity, black spruce (*Picea mariana*) tree cover, and wetlands, and covariates for pre-existing anthropogenic conditions, such as provincial highways (hereafter primary roads) and linear features associated with no or unknown levels of human use. We then used Schwarz's information criterion (SIC; Schwarz 1978) to determine whether covariates related to human use during winter oil exploration improved the models and hence whether human use affected resource selection. The human-use covariates considered were: (1) distance to secondary exploration roads (hereafter secondary roads), which provide frequent access to winter exploration camps and facilities; (2) distance to tertiary exploration roads (hereafter tertiary roads), which provide less frequent access to remote parts of the study area; and (3) binary covariates for locations within 250 m of secondary and tertiary roads (as per Dyer *et al.* [2001] and Sorensen *et al.* [2008]).

Evaluating physiological stresses and human use

We similarly evaluated how physiological (nutritional and psychological) stress indices in caribou and moose varied with each species' base RSPF using linear regression. Forward model selection by SIC was used to add covariates associated with human use in estimating the final model. We expected T3 and GC hormone concentrations to be associated with base RSPF, indicating how habitat choice reflects physiological condition. We then quantified how human-use levels across the landscape affected physiological stress, after controlling for the base RSPF, by adding proximity to active roads and levels of human activity to the model (session A = oil crews arrive, low activity; B = moderate activity; C = peak activity; D = low activity, oil crews depart; WebFigure 1). We hypothesized that physiological stress should increase

near primary roads, independent of activity sessions A–D. However, for all secondary and tertiary roads, physiological stress should increase with the human activity level, as reflected by activity session.

Evaluating wolf predation

We investigated wolf predation by first addressing the common presumption that habitat selection by predators depends on where prey species are likely to occur (Keim *et al.* 2011). Wolf diet composition was evaluated from prey hair found in the wolf scats (Shores and Wasser unpublished data; WebPanel 1). We then examined how each of the species affect wolf habitat selection by using RSPFs for deer, moose, and caribou, averaged across a 5.3-km² areal extent, as covariates for estimating wolf resource selection.

Measuring population sizes

The ability to reliably estimate changes in caribou, moose, and wolf abundance is critical in evaluating the impacts of current and future human activities on this ecosystem, as well as mitigating observed declines in caribou. We used genetic, scat-based CMR analyses to estimate caribou, moose, and wolf population sizes in 2006 and 2009 (WebPanel 1).

Results

Functional habitat loss and resource selection

The base RSPF for caribou (WebTable 5) indicates positive selection for wetlands (as defined by Alberta's Wetland Inventory), less topographically complex terrain (flatter locales), locations farther from primary roads, linear features associated with no or unknown levels of human use, areas of open black spruce tree cover, and pine–lichen ecosystems; for additional information regarding definitions of resource selection covariates, see WebTable 3. Pine–lichen and black spruce-related covariates were the least influential, based on SIC differences, suggesting that resource selection by caribou may be driven less by these forage-related resources than by other mechanisms, such as predator avoidance. Importantly, distance to linear features having no or unknown levels of human use was not selected for inclusion in the caribou model based on SIC, implying that caribou are not experiencing functional habitat loss from linear features alone. Caribou did avoid areas near primary roads, indicating that functional habitat loss may have more to do with human use than with the linear features themselves.

In contrast, the base RSPF for moose (WebTable 5) indicates positive selection for sites dominated by shrubs, associated with recent wildfires (ie within the previous 40 years), located within 100 m of streams and lakes (henceforth riparian proximity), and associated with lower densi-

ties of coniferous tree cover. Moose avoided linear features with no or unknown levels of human use and sites near primary roads. Based on SIC differences, moose selection was foremost related to those covariates associated with increased browse (ie lower density coniferous tree cover, shrub dominance, recent wildfires, and riparian proximity).

Human-use covariates related to winter oil exploration contributed further in explaining resource selection by caribou. The selection probability was reduced by proximity to secondary and tertiary roads (Δ SIC = -20.4), with reduction from secondary roads (60%) nearly twice as that from tertiary roads (35%; Figure 1). Areas within 250 m of these features did not improve the base model (Δ SIC = $+13.6$; WebPanel 1). Also, caribou showed increased displacement from lower RSPF areas when closer to secondary and tertiary roads; this tendency was greater for secondary than for tertiary roads (Figure 1). In fact, caribou selected linear features with no human use, providing additional support for the hypothesis that functional habitat loss in caribou is more related to the degree of human use than to the presence of linear features alone.

Moose appear to have lower sensitivity to human activity than do caribou. Distance to both secondary and tertiary roads did not add to the parsimony of the base RSPF model for moose (Δ SIC = $+6.0$), although areas within 250 m of these features did improve the base model (Δ SIC = -20.6). Thus, the effect of exploration roads for moose (in contrast with that for caribou) does not reach beyond several hundred meters.

Physiological stresses resulting from human use

In regressing log-hormone concentrations over various covariates, the final model consisted of base RSPF, primary roads, oil exploration (OE) roads (secondary and tertiary roads combined), human activity session, and the interactions between these variables. Table 1 shows the coefficient estimates and standard errors for each variable in the final T3 and GC models for caribou and moose. The SIC scores after adding each new variable to the model are shown in WebTable 9. For caribou T3, the negative coefficient for the base RSPF covariate indicated that nutrition was relatively poor in high RSPF areas as compared with nutrition in low RSPF areas. This corroborates the RSPF results, which suggest that caribou selected areas more for security than nutrition. Nutritional and psychological stresses decreased (increasing T3 and decreasing GC, respectively) with distance from primary roads. By contrast, nutritional stress tended to increase (decreasing T3, increasing GC) with distance from OE roads. SIC scores showed marked effects of sampling session on T3 and GC as a main effect and when interacting with base RSPF and OE roads. Psychological stress was highest (high GC) and nutrition poorest (low T3, high GC) when humans were most active in the landscape (sessions B and C), but caribou recovered as oil crews left the area (session D; WebFigure 1). These find-

ings were also supported by the interactions between session and base RSPF, between session and OE roads, and between OE roads and base RSPF (WebFigures 4 and 5). Caribou nutrition was best (high T3) in areas with low RSPF values that were far from OE roads, but nutrition diminished with increasing human activity – ie proximity to OE roads and particularly in sessions B and C, when humans were most active (WebFigure 4).

Caribou GCs were consistently highest in the high RSPF areas, except when farthest from OE roads during sessions when humans were most active (WebFigure 5). This is also consistent with nutrition being best in low RSPF areas but, more importantly, suggests that high RSPF areas become increasingly psychologically stressful when humans are present – likely because the conditions at high RSPF sites improve sensory detection across the landscape (flat wetland conditions having less canopy cover), thus enabling caribou to better detect humans.

For moose, base RSPF was significantly positively correlated with T3 and GC (Table 1). This is consistent with our RSPF findings that moose are selecting for forage over security. There were no significant effects of primary or OE roads as main effects. However, density of linear features was positively correlated with T3 (Table 1), which is consistent with hypotheses that linear features increase moose forage. Inclusion of human activity sessions markedly improved the model. Nutrition was poorest in session C and best in session D, and the positive correlation between RSPF and T3 disappeared in session D. GCs in moose did not show a strong pattern by activity session, except as an interaction with OE roads. GCs were highest when closest to OE roads in sessions B and D only (Table 1).

Wolf predation

Deer, moose, and caribou comprised 96% of the winter diet of wolves. After biomass correction, 24% of wolf diet was composed of moose, 11% of caribou, and 65% of deer (Shores and Wasser unpublished data). In a nearby study area, Latham (2009) found similar results for the wolf diet in both the snow and snow-free seasons.

The resource selection model for wolf indicates positive selection for linear features and for deer habitat (high deer RSPF). By contrast, neither the moose nor caribou resource selection models positively contributed to the wolf RSPF (WebFigure 7). Importantly, the resource selection models for deer and caribou were negatively correlated ($r = -0.5$) across the landscape. Wolves seemingly target deer in our study area, and the strong negative correlation between deer

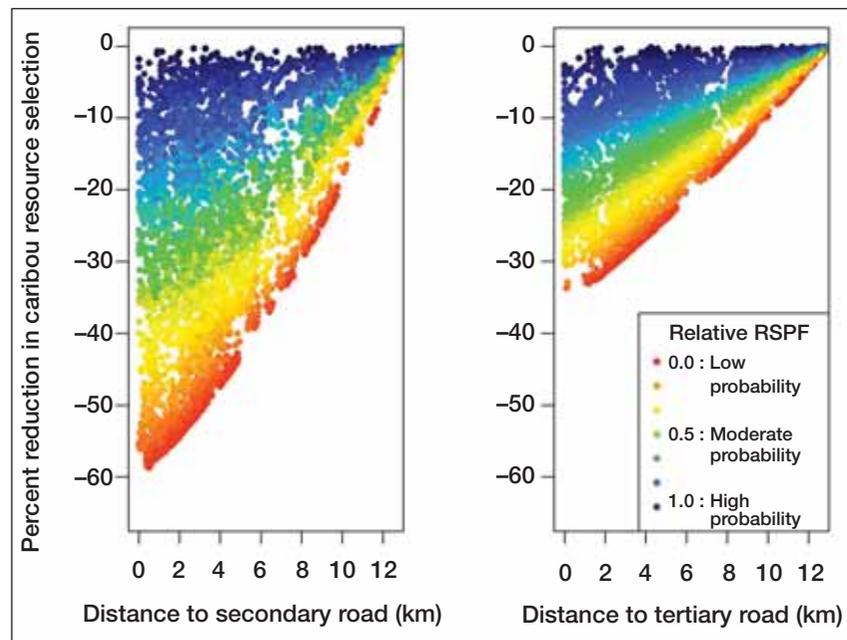


Figure 1. Influence of proximity to winter oil exploration roads on resource selection by caribou. Relative RSPF is the caribou resource selection model with the effect of secondary or tertiary roads fixed at 13 km, where only a marginal road effect results. Resources having a high probability of selection (blue) are relatively uninfluenced by road distance, whereas lower probability resources (green to orange) become highly influenced.

and caribou RSPFs suggests that wolf preference for deer draws wolves away from prime caribou habitat (WebFigure 2).

Monitoring population sizes

On the basis of CMR analyses, we estimate 330 caribou, 387 moose, and 113 wolves in our study area in the year 2009. The coefficients of variation surrounding these population estimates are notably small: 7.5% in caribou, 14% in moose, and 20% in wolf. Genotyping identified 208 unique caribou, 174 unique moose, and 69 unique wolves from the scat samples obtained in 2009. Our CMR estimate for caribou is considerably higher than current expectation for the entire ESAR caribou range (90–150 animals), which includes five additional caribou ranges surrounding the study area. We were unable to detect any significant changes in the 2006 and 2009 population estimates for any of the species studied (Figure 2), although the wide confidence interval in the 2006 caribou population estimate could have masked small changes in their population size. The Otis models' closure assumption was probably violated for wolves and moose but not for caribou in either year. As a consequence, population sizes for wolves may be somewhat lower and for moose somewhat higher than those indicated by the estimates (WebPanel 1).

Discussion

Projections of rapid declines in caribou abundance have created a sense of urgency for wildlife management actions, with intentional removal of wolves advocated as

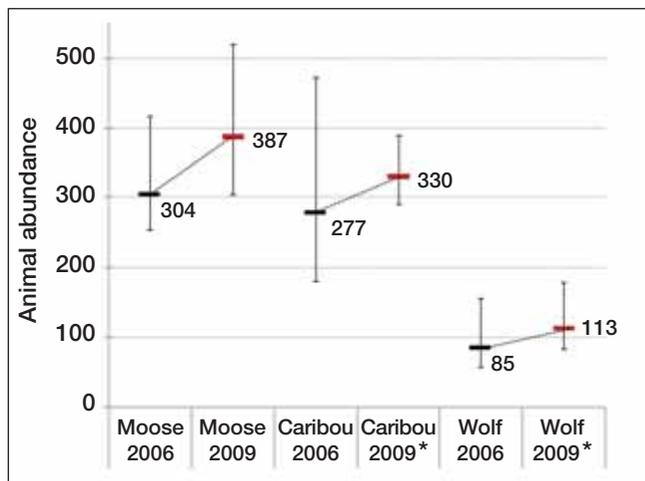


Figure 2. CMR abundance estimates for moose, caribou, and wolf obtained from DNA in scat. Precision of population estimates markedly improved with RSPF-guided sampling in caribou and wolf, conducted by increasing the sampling intensity of high RSPF resource types in 2009. Asterisk indicates RSPF-guided sampling. Improved DNA amplification also enhanced precision in caribou. Maximum likelihood abundance estimates (labeled) and 95% confidence intervals are depicted for each species; horizontal black and horizontal red dashes indicate 2006 and 2009 estimates, respectively.

the most effective tool to curb such declines in this region (Schneider et al. 2010). However, our data indicate that:

- (1) caribou population size is more than double current perception for this area (Cichowski 2010), and caribou, moose, and wolf abundances did not significantly change over our 4-year study period;
- (2) wolves are primarily targeting deer within this study area (based on diet and resource selection);
- (3) functional habitat and physiological health of

caribou are negatively affected by the degree of human activity on the landscape.

These results do not suggest that caribou populations are free from risk in the Alberta oil sands, nor do they imply that management action is unwarranted. They do, however, indicate that more time is available than previously thought for managers to arrive at the best solutions to facilitate caribou recovery in this region and that managing human use may prove more effective than removing wolves.

The current management priority of wolf removal is likely to reduce caribou mortality in the short term. However, a predator release effect of deer is also likely. The resultant rapid expansion of deer populations could,

Table 1. Coefficient estimates and standard errors for each variable in the final general linear model for effects on GC and T3 in caribou and moose

Model	bRSPF	Primary roads	eRoads	Session A–D (D = reference)	Session x bRSPF	Session x eRoads	eRoads x bRSPF	eRoads x bRSPF x session
Caribou T3 (n = 350)	-0.62	13.5	-17.6	74.0 (A)	0.24 (A)	24.99 (A)	-0.06	0.072 (A)
	<i>0.17</i>	<i>3.82</i>	<i>5.98</i>	22.9	<i>0.16</i>	<i>6.7</i>	<i>0.05</i>	<i>0.058</i>
				-78.0 (B)	-0.39 (B)	4.8 (B)		-0.053 (B)
				32.0	<i>0.21</i>	<i>9.37</i>		<i>0.078</i>
Caribou GC (n = 388)	0.68	-18.0	15.7	31.7 (A)	-0.10 (A)	-30.9 (A)	-0.11	
	<i>0.18</i>	<i>4.25</i>	<i>6.07</i>	27.1	<i>0.19</i>	<i>7.03</i>	<i>0.0361</i>	
				-104 (B)	-0.55 (B)	22.2 (B)		
				32.8	<i>0.21</i>	<i>8.97</i>		
Moose T3: (n = 300)	0.44	-4.85	LFD: 107.0	-51.1 (A)	0.29 (A)			
	<i>0.13</i>	<i>3.09</i>	<i>26.2</i>	25.7	<i>0.22</i>			
				5.2 (B)	-0.21 (B)			
				25.2	<i>0.20</i>			
Moose GC (n = 304)	0.46	-5.07	-7.71	-42.75 (A)	0.21 (A)	29.13 (A)		
	<i>0.14</i>	<i>3.55</i>	<i>5.30</i>	25.30	<i>0.23</i>	<i>7.31</i>		
				67.52 (B)	0.41 (B)	-19.28 (B)		
				26.28	<i>0.21</i>	<i>6.82</i>		
			39.15 (C)	0.20 (C)	6.92 (C)			
			27.16	<i>0.22</i>	<i>7.77</i>			

Notes: All values (excluding sample sizes) multiplied by 1000. n = sample size; LFD = linear feature density, instead of roads, significant for moose T3 only; eRoads = exploration roads; bRSPF = base RSPF. Standard errors are italicized and provided below each coefficient in the table.

in turn, lead to a cascade of problems that are much more difficult to manage than current concerns (eg disease transmission, high-amplitude predator–prey oscillations, or marked alterations in vegetation; Ripple and Beschta 2006; Krumm *et al.* 2010).

Management should prioritize and exhaust feasible actions to control human use on this landscape before triggering more extreme actions, such as predator removal. More specifically, we recommend that human activity be physically and temporally clustered on the landscape during periods of oil exploration. Roads and temporary camps should be located in areas that provide better visual and sound barriers (eg with placement buffered by forested and complex terrain, and away from caribou forage). Traffic patterns should be consolidated by minimizing the number of secondary roads and by shifting as much traffic as possible to those roads. These recommendations will become especially important when designing future all-season access roads and infrastructure. Continued monitoring after such mitigations are in place will allow managers to quickly assess their efficacy and change course if needed.

We further recommend that several strategic caribou ranges in Alberta be selected for detailed long-term monitoring, using the methods described here. Simply monitoring caribou population size is insufficient for managing caribou in the ecosystem. Impacts on resource selection and its physiological consequences should also be examined for interacting predator and prey species, to identify problems more quickly and to help explain any observed population changes in this complex ecosystem.

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