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

Samuel K Wasser^{1*}, Jonah L Keim², Mark L Taper³, and Subhash R Lele⁴

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 mid-March 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, 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 affects 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.* in press). 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 were 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 den-

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 when oil crews left the area (session D; WebFigure 1).

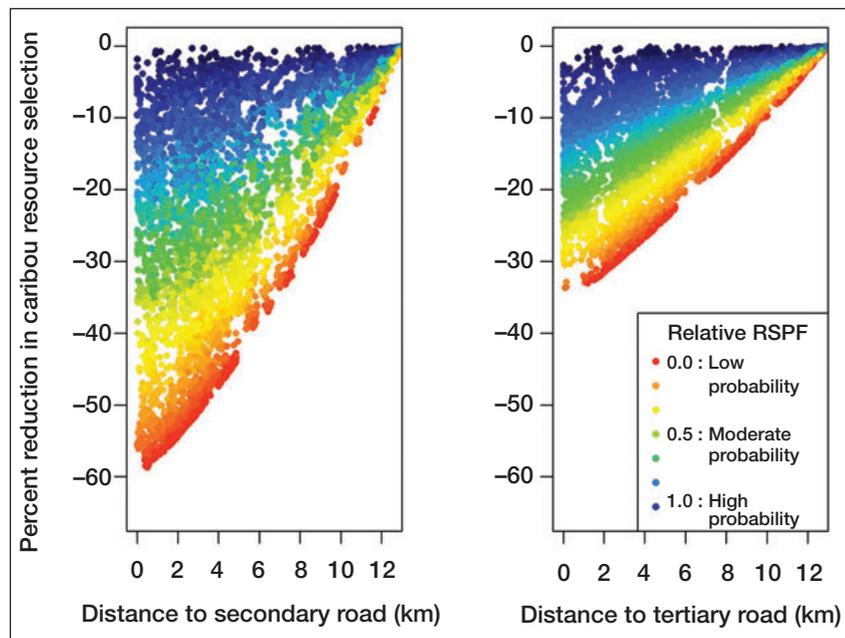


Figure 1. Influence of proximity to winter oil exploration roads on resource selection by caribou. Relative RSPF is the caribou resource selection model with the effect of secondary or tertiary roads fixed at 13 km, where only a marginal road effect results. Resources having a high probability of selection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

These findings 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 and caribou

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

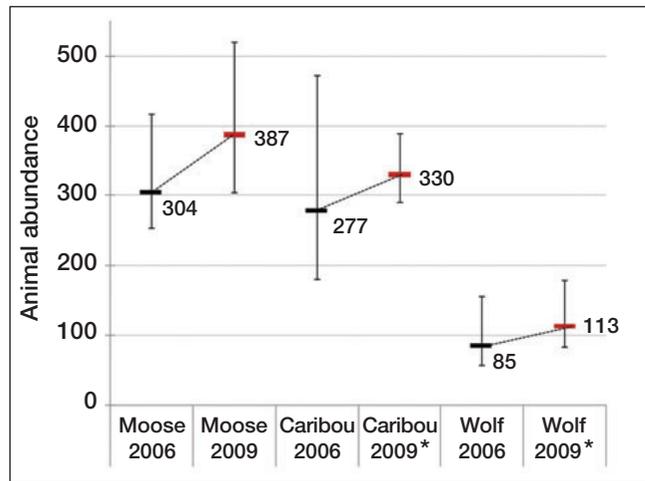
Monitoring population sizes

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> |
| | | | –34.6 (C) | 0.33 (C) | 7.34 (C) | | –0.11 (C) | |
| | | | 22.7 | <i>0.18</i> | <i>7.38</i> | | <i>0.067</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> | | |
| | | | 173 (C) | –0.23 (C) | –20.5 (C) | | | |
| | | | 24.4 | <i>0.20</i> | <i>7.27</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> | | | |
| | | | –275.0 (C) | 0.50 (C) | | | | |
| | | | 25.4 | <i>0.23</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 are 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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■ References

Alberta Caribou Committee. 2009. Athabasca caribou landscape management report. Edmonton, Canada: Alberta Caribou Committee. www.albertacariboucommittee.ca/PDF/Athabasca-Caribou.pdf. Viewed 11 Apr 2011.

Ball MC, Pither R, Manseau M, *et al.* 2007. Characterization of target nuclear DNA from faeces reduces technical issues associ-

ated with the assumptions of low-quality and quantity template. *Conserv Genet* 8: 577–86.

Bradshaw CJA, Boutin S, and Herbert DM. 1997. Effects of petroleum exploration on woodland caribou in northeastern Alberta. *J Wildlife Manage* 61: 1127–33.

Cichowski D. 2010. Status of the woodland caribou (*Rangifer tarandus caribou*) in Alberta: update 2010. Edmonton, Canada: Alberta Sustainable Resource Development. Wildlife Status Report Number 30 (update 2010).

Douyon L and Schteingart DE. 2002. Effect of obesity and starvation on thyroid hormone, growth hormone, and cortisol secretion. *Endocrin Metab Clin* 31: 173–89.

Dyer SJ, O'Neill JP, Wasel SM, and Boutin S. 2001. Avoidance of industrial development by woodland caribou. *J Wildlife Manage* 65: 531–42.

James ARC and Stuart-Smith AK. 2000. Distribution of caribou and wolves in relation to linear corridors. *J Wildlife Manage* 64: 154–59.

Keim J, DeWitt P, and Lele S. Predators choose prey over prey habitats: evidence from a lynx–hare system. *Ecol Appl*. In press. doi:10.1890/10-0949.1.

Kitaysky AS, Romano MD, Piatt JF, *et al.* 2005. The adrenocortical response of tufted puffin chicks to nutritional deficits. *Horm Behav* 47: 606–19.

Krumm CE, Conner MM, Thompson Hobbs N, *et al.* 2010. Mountain lions prey selectively on prion-infected mule deer. *Biol Lett* 6: 209–11.

Latham ADM. 2009. Caribou–primary prey–wolf relationships in low-productivity peatland complexes in northeastern Alberta (PhD dissertation). Edmonton, Canada: University of Alberta.

Lele SR and Keim JL. 2006. Weighted distributions and estimation of resource selection probability functions. *Ecology* 87: 3021–28.

McLoughlin PD, Dzus E, Wynes B, and Boutin S. 2003. Declines in populations of woodland caribou. *J Wildlife Manage* 67: 755–61.

Ripple WJ and Beschta RL. 2006. Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. *Forest Ecol Manag* 230: 96–106.

Schneider RR, Hauer G, Adamowicz WL, and Boutin S. 2010. Triage for conserving populations of threatened species: the case of woodland caribou in Alberta. *Biol Conserv* 143: 1603–11.

Schwarz G. 1978. Estimating the dimension of a model. *Ann Stat* 6: 461–64.

Sorensen T, McLoughlin PD, Hervieux D, *et al.* 2008. Determining sustainable levels of cumulative effects for boreal caribou. *J Wildlife Manage* 72: 900–05.

Stuart-Smith KA, Bradshaw CJA, Boutin S, *et al.* 1997. Woodland caribou relative to landscape patterns in northeastern Alberta. *J Wildlife Manage* 61: 622–33.

Terborgh J and Estes JA (Eds). 2010. Trophic cascades. Washington, DC: Island Press.

Wasser SK, Cristóbal-Azkarate JA, Booth RN, *et al.* 2010. Non-invasive measurement of thyroid hormone in feces of a diverse array of avian and mammalian species. *Gen Comp Endocr* 168: 1–7.

Wasser SK, Davenport B, Ramage ER, *et al.* 2004. Scat detection dogs in wildlife research and management: application to grizzly and black bears in the Yellowhead ecosystem, Alberta, Canada. *Can J Zool* 82: 475–92.

Wasser SK, Hunt KE, Brown JL, *et al.* 2000. A generalized fecal glucocorticoid assay for use in a diverse array of nondomestic mammalian and avian species. *Gen Comp Endocr* 120: 260–75.

White GC. 2009. MARK version 6.1. <http://warnerncr.colostate.edu/~gwhite/mark/mark.htm#Documentation>. Viewed 11 Apr 2011.

WebPanel 1. Detailed methods and results**DNA extraction and amplification**

At the time of the 2006 collection, each scat sample was split in half, with one half stored frozen and the other in 20% dimethyl sulfoxide (DMSO) in a tris-EDTA (ethylenedinitrilotetraacetate) buffer (Wasser et al. 2004) for later laboratory analyses. Moose and wolf DNA were extracted from the DMSO-stored samples using methods detailed in Wasser et al. (2004). A different extraction method, modified from Ball et al. (2007), was required for caribou because of high concentrations of polymerase chain reaction (PCR) inhibitors contained in their lichen-rich diet. Caribou scat samples were freeze-dried, resuspended in phosphate-buffered saline (PBS), and then processed for DNA analysis by swabbing the frozen slurry with a cotton swab. This removed the DNA while leaving most of the PCR inhibitors behind. DNA was liberated from the cotton swab by overnight proteinase K digestion followed by purification using silica absorption and standard DNA extraction protocols from a Qiagen DNeasy 96 tissue kit. This method provided the first reliable caribou genotypes ever acquired from scat. However, additional modifications, described below, more than doubled our mean amplification success of microsatellite DNA in the 2009 (90%) caribou samples compared to 2006 (42%).

In 2009, DNA from all three species was collected from fresh frozen samples by swabbing the mucosal surface of the scat using a cotton-tipped applicator. This carried substantially less of the scat matrix (including PCR inhibitors) into the DNA extractions in 2009 compared to 2006. The cotton applicator, which included very little of the scat matrix, was processed directly using a proteinase K digestion and column purification with the Qiagen tissue extraction protocol. PCR was also performed within days of the extraction in 2009, versus several weeks in 2006.

Caribou samples were first analyzed for species ID using the HSF21 and LTPROB mtDNA primers (Wasser et al. 1997); 5% of presumed caribou scats were actually deer scats. Wolf samples were analyzed for species ID using the hinfl digest of the LI5774-HI6498 (Foran et al. 1997); 11% of scats presumed to be wolf scats were actually from coyotes. All non-target scats (2.5% of all samples) were discarded. Species ID was deemed unnecessary on moose samples because moose scat is visually distinct.

Samples were next assayed for six species-specific microsatellite loci (WebTable 1). Allele frequencies were consistent with Hardy-Weinberg equilibrium (HWE) at all loci examined. Samples were extracted twice to compensate for the uneven distribution of DNA in scat (Wasser et al. 2004), with each extract PCR amplified at least twice to minimize allelic dropout. Confirmation of heterozygous alleles required both alleles to be observed at least twice, whereas confirmation of homozygous alleles required the single allele to be observed at least three times in the same sample. Single locus exclusion genotypes were also examined for the frequency of homozygotes and found to be consistent with expectation.

WebTable 2 presents data quality estimates from CERVUS (Kalinowski et al. 2007) analyses of caribou, moose, and wolf samples in 2006 and 2009, including number of unique individuals

genotyped, summed P_{ID} scores from CERVUS, as well as sample quality estimates (number of matches with sufficient data, % samples amplified to ≥ 3 loci required for individual ID, mean number of loci used for match). P_{ID} is the number of times that two distinct individuals from the population are expected to be identified as one in this genetic sample. The interpretation of P_{ID} scores across years is illustrated for caribou. In 2006, the summed P_{ID} is 0.073 for 47 matches. Thus, the probability that there are no false matches in the entire dataset is 0.930, while the probability of there being no more than one false match is 0.997 (ie only about one out of about 671 matches will be a false match). In 2009, the summed P_{ID} is 0.019 for 354 matches, giving a probability that there are no false matches in the entire dataset as 0.981, while the probability of there being no more than one false match is 0.9998 (ie only about one out of 19631 matches will be a false match). Results indicate that coalescent misidentifications are rare in our data, making it legitimate to model the total as a Poisson random variable. These calculations are for false matches of unrelated individuals in the population. This assumption seems reasonable for caribou because they very rarely have more than a single calf in this habitat and are not monogamous. False matches with full siblings, if present, are more probable (Kalinowski et al. 2006). Twinning occurs more frequently in moose, but is still not common. Multiple pup litters is the rule for wolves, making samples from a wolf social structure somewhat more prone to false matches. False matches, if present, would bias abundance estimates toward the lower boundary of the population size.

The probability that mismatch errors will create the appearance of two individuals where there is only one (the “shadow effect”) is also well controlled. The only amplification error that has been observed is allelic dropout. We estimate that the proportion of amplifications of heterozygous samples that result in the dropout of one or the other allele is about 0.07. Under our genotyping protocol, for a sample truly heterozygous at a locus to be identified as homozygous, the same dropout error would need to occur three times, which only has a probability of about 9×10^{-5} . For samples heterozygous at all six loci, a shadow individual is only expected to be generated once in about 1851 genotypings.

Hormone extraction

Glucocorticoid (GC) (Wasser et al. 2000) and thyroid (T3) hormone (Wasser et al. 2010) metabolites have been validated and measured in feces of a wide variety of mammals, including the three study species. Hormone extractions were performed using the pulse vortex method described in Wasser et al. (2010). Briefly, 15 mL of 70% ethanol was added to 0.1 g of freeze-dried and thoroughly homogenized fecal powder, vortexed on a multitube pulsing vortexer for 30 minutes at one pulse per second (Glas-Col, Terre Haute, IN), and then centrifuged for 20 minutes at 2200 rpm. The supernatant was decanted from the fecal pellet and stored in an airtight tube. Another 15 mL of 70% ethanol was added to the original pellet and the extraction process was repeated a second time. The supernatant from the second extraction was combined with the first and then stored at -20°C until assayed.

WebPanel 1. Detailed methods and results – continued

All hormone concentrations were expressed per gram dry feces (ng g^{-1}) to control for potential dietary variation in hormone excretion (Wasser *et al.* 1993). Samples outside 15–85% bound on the standard curve, or with a coefficient of variation between duplicate pairs $\geq 10\%$, were re-assayed at appropriate concentrations.

Serial dilutions paralleled respective standard curves, indicating that GC and T3 were being reliably measured across their respective range of concentration. For T3, 50% binding occurred at a 1:10 dilution for moose, 1:20 for caribou, and 1:30 for wolf. Accuracy studies produced slopes of 1.05 ($r^2 = 0.99$) for moose, 0.98 ($r^2 = 0.98$) for caribou, and 1.08 ($r^2 = 0.99$) for wolf, illustrating that fecal extracts were not interfering with T3 measurement precision in these species (Wasser *et al.* 2010). For GC, 50% binding occurred at 1:30 for moose, 1:40 for caribou, and 1:60 for wolf. Accuracy studies produced slopes of 0.901 ($r^2 = 0.999$) for moose, 0.90 ($r^2 = 0.999$) for caribou, and 1.04 ($r^2 = 0.999$) for wolf.

Resource selection**Caribou and moose**

Resource selection analysis was conducted at a species-specific population level rather than at an individual level. We obtained data from a large number of unique individuals, but with a correspondingly low number of recaptures. While this sampling makes it unlikely that any single individual would be overrepresented in our population-level analyses, it also limits analyses at the individual level due to small sample size. The used (2006 and 2007 scat locations) and available (7000 random points) locations were equally constrained by the sampling routes to account for sampling bias, with the analyses matched by sampling year and session (WebFigure 1) to account for temporal variability. Constraining availability in this way is common in resource selection studies (Arts *et al.* 2008).

The resource selection models assume that resource conditions within the sampled extents can be equally encountered by the study species. Multi-model inference using two model forms, the exponential resource selection function and the logistic resource selection probability function, were considered. Resource selection models were estimated using maximum likelihood methods (Lele and Keim 2006) with the final model form and covariates selected using Schwarz information criterion (SIC; Schwarz 1978) – often referred to as Bayesian information criterion (BIC) in ecological studies. Numerous studies now compare the performance of the bias-corrected Akaike's information criterion (AICc) and SIC (eg Taper 2004; Astrap *et al.* 2008; Raffalovich *et al.* 2008; Murtaugh 2009). While no criterion is superior for all model types and purposes, a consensus is emerging: the SIC is best for identifying variables of importance, while the two criteria perform very similarly for selecting models for prediction. As we are interested in both important variables and prediction, we use the SIC as our model selection criterion.

Base resource selection models were fit for both caribou and moose. The covariates in the base models specifically related to winter during the sampling year, and purposely ignored oil explo-

ration roads associated with human use. Once the final base models for each species were fit, the covariates related to the winter exploration roads were then added to see if they improved model fit for each species.

The covariates considered in the resource selection analysis for all species are defined in WebTable 3. WebTable 4 provides the SIC values for the various caribou and moose models considered. The parameter estimates and standard errors for the final caribou and moose resource selection models are presented in WebTable 5.

Wolf

Wolf resource selection was estimated from the 2006 and 2007 scat samples ($n = 183$) using the methods detailed above, except that the used and available data were matched by year in the estimation because we were not interested in session effects. In estimating resource selection by wolves, we considered the RSPFs for caribou, moose, and deer since these three species collectively made up 96% of the wolf diet, based on our analyses of hair found in wolf scat (Shore and Wasser unpublished data). Linear features were also considered. We used the full RSPF models for caribou and moose (WebTable 5) along with a deer RSPF model (Keim *et al.* unpublished data; WebTable 6). The deer RSPF was estimated from a large sample of winter snow tracking data collected within and surrounding the study area, using methods from Keim *et al.* (in press). The deer RSPF was then regressed against a subset of data (213 deer tracks, 115 km of transect) collected in the study area to demonstrate that the RSPF is proportional to winter habitat use by deer in the study area (WebFigure 2).

Because wolves selectively defecate to mark their territories, we measured broad-scale metrics of prey distribution by averaging the RSPFs of moose, caribou, and deer across an extent of 5.3 km^2 surrounding each used and available location. We assume that the wolf scat locations, although potentially biased at finite scales due to territorial marking behavior, are representative of their distribution patterns across the broader scale we considered. We acknowledge that territorial marking by wolves could bias the selection model toward linear features. However, we retained linear features in the model because (1) an unusually high proportion of scat was found on these features (44% of the samples), (2) wolf telemetry from the area indicates a strong selection for linear features (James and Stuart-Smith 2000), and (3) the presence of linear features in the model did not influence the relative inferences on the prey species (tested by estimating the model with and without linear features; data not shown).

WebTable 7 provides the SIC values for the various models considered. The parameter estimates and standard errors for the final wolf resource selection model are presented in WebTable 8.

The best fit model based on SIC includes the RSPF covariates for both deer and caribou. However, because the deer and caribou RSPF covariates considered in the wolf model were highly and negatively correlated ($r = -0.5$) and because a negative relation was found between wolf selection and the caribou RSPF without influencing a strong positive relation with the deer RSPF

WebPanel 1. Detailed methods and results – continued

(WebTable 8; WebFigure 3), we suggest that the most appropriate final model for wolves is: LF + Deer RSPF (the second best fit model based on SIC).

Stress and nutrition analyses

Glucocorticoid (GC) and thyroid hormone metabolite (triiodothyronine, T3) concentrations assayed from the 2006 scat samples were used as response variables of physiological condition. As detailed in the main manuscript, 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 Schteingart 2002). Both response variables were transformed to the log scale. Because hormones are typically excreted in scat 24 hours after secretion into the blood (Wasser *et al.* 1994, 2000), we averaged applicable covariates across a 24-hour movement radius of each scat location (5.3 km²).

We used linear regression to evaluate how T3 and GC vary with habitat choice (base RSPF) in caribou and moose. To account for possible range of movement in a 24-hour period, we used the average of the resource selection probability and measured linear feature distance within 1300 m (or 5.3 km²) surrounding each scat location. Forward model selection by SIC was then used to add covariates associated with human use in estimating the final model. Human-use variables were added in the following order:

- (1) distance to provincial highways (termed primary roads: continuous variable; WebTable 9);
- (2) distance to secondary and tertiary roads combined (termed oil exploration roads: continuous variable; WebTable 9);
- (3) linear density (km/5.3 km²) of high and low human-use roads, seismic lines, power lines, and pipe lines (continuous variable; only significant in the Moose T3 model, where effects of roads were not significant);
- (4) sampling session (discrete variable with reference category set to Session D; sampling sessions were chosen to correspond to the number/activity of workers on the landscape: session A = oil crews arrive, low activity; B = moderate activity; C = peak activity; D = low activity, oil crews pack up and leave; WebFigure 1);
- (5) statistical interactions between all main effects.

Sample size varied by analysis and depended upon reliable assays of T3 and GC (sample sizes: Caribou T3 = 350, Caribou GC = 388, Moose T3 = 300, Moose GC = 304). WebTable 6 provides the final SIC models for predicting thyroid (T3) and glucocorticoid (GC) hormone levels in caribou and moose.

Mark–recapture analysis

Individual identities and sample matches of genotyped samples were assigned using CERVUS version 3.0.3 (Kalinowski *et al.* 2007). Matched samples were defined as having identical genotypes at a minimum of three of the six loci examined, with no mismatched genotypes. However, the majority of matches occurred on five or more loci (WebTable 2). These data were then analyzed using mark–recapture methods, wherein detection of the same

genotyped individual one or more times in a single sampling session was considered only a single capture or recapture.

Population size estimates were made using Program MARK (White 2009). Six models in the Otis *et al.* (1978) family were fit using maximum likelihood. Using Program MARK notation (Otis *et al.* 1978) these models can be denoted as: {N, p(.) = c(.)}, a model with a population size parameter (N), and a single parameter for probability of first capture (p) and probability of recapture (c) that is constant over all sessions; {N, p(.), c(.)}, first capture and recapture probabilities are distinct, but constant over sessions; {N, p(.), c(t)}, constant first capture probability with recapture probabilities that vary over sessions; {N, p(t), c(.)}, first capture probability varies with session while recapture probability is constant; {N, p(t) = c(t)}, a single parameter for first capture and recapture probabilities within a session that varies over sessions; and {N, p(t), c(t)}, first capture and recapture probabilities are distinct within a session with both varying over sessions. Model selection was made using the SIC criterion (Schwarz 1978; WebTable 10). Models with capture parameters estimated at either the 0 or 1 boundary are considered not estimable and are not included in the candidate model sets.

Because of the nature of our sampling, individual heterogeneity in capture and recapture probability was not anticipated to be large. This was confirmed by comparing for each year and species SIC values for the best model without heterogeneity with the corresponding model as a two group finite mixture. In all cases, the model without heterogeneity was strongly favored over the model with heterogeneity, with Δ SIC values ranging from 5.6 to 28.9.

Abundance estimates were not converted to density estimates because it has long been known that naïve estimates of density from mark–recapture estimates – those that estimate density by dividing estimated population size by grid area – are biased high by what is known as the “edge effect” (Dice 1938). Often, this bias is enormous (Wilson and Anderson 1985).

All models are the closed population model, assuming that animals neither enter nor leave the population during the study period. Closure was tested by both the Otis *et al.* (1978) method and the Stanley and Burnham (1999) method using Program CloseTest (Stanley and Richards 2004). Neither test indicates closure assumption violations in either year for caribou. However, both tests indicate closure violations are possible for wolf and moose in 2009. Inspection of the chi-square components of both closure tests indicate that it is not likely that any wolves entered the study area over the sampling period, but some individuals may have died or left the area. Chi-square components indicate that some individual moose may have entered the study between session 2 and 3. The consequences of these assumption violations are that the wolf population estimate is likely to be biased high and the moose population estimate low (Kendall 1999). The magnitude of these biases was checked by creating a legitimate Lincoln-Peterson two sample estimate. This is done by collapsing the sessions below and above the transition with the loss or gain into single sessions and recalculating abundances using the Lincoln-Peterson method (Kendall 1999). In this case, this meant

WebPanel 1. Detailed methods and results – continued

collapsing sessions B–D into one session for the wolf data and sessions A–C into one session for moose. Although changing in the expected directions, the revised abundance estimates hardly differed from those reported in WebTable 11 (Wolf 2009 LP estimate 128, 95% confidence interval [CI]: 82–253; Moose 2009 LP estimate 535, 95% CI: 364–851).

Improved precision/guided sampling

It is a general feature of the mark–recapture models used in this analysis that the variance in the estimate of N decreases monotonically with increase in any sample detection probability. As a consequence, any sampling design features that increase detection probability ($p(t)$) will increase the precision of our estimates. In 2006, transects were selected to maximize the diversity of habitats covered. In 2009, in order to increase detection probabilities, sampling was directed using the caribou RSPF estimated previously. Extra effort was also put into sampling linear features to increase wolf detection.

We define a detection cell (as distinct from a sampling cell) as a small area that dogs search, which can be considered an atom (ie the smallest unit) of resource selection by our target species. By definition, the probability of selection is the probability that a location having a given resource combination, if encountered, will be used by an animal (Lele and Keim 2006). Consequently, if we assume that individuals use the environment in a fine-scale fashion, then the proportion of time that an individual spends in a detection cell is proportional to the selection probability of the cell, r_k .

The probability, d_k , that an individual is detected in a cell should be a monotonic function of the time spent in the cell, ranging from 0 if the individual never enters the cell to 1 if the individual spends a great deal of time in the cell. However the cell detection probability is determined, the detection probability of the j^{th} sample, p_j , is:

$$p_j = 1 - \prod_{k=1}^{D_j} (1 - d_k) .$$

where D_j is the total number of detection cells along all transects in a sample period. As d_k are known to all be small this can then be approximated well by:

$$p_j \cong 1 - \exp \left(- \sum_{k=1}^{D_j} d_k \right) .$$

This can heuristically be further approximated by:

$$p_j \approx \sum_{k=1}^{D_j} d_k$$

Although this approximation probably will not be useful for estimation it does demonstrate that sample detection probability can be increased both by increasing the total transect length (D_j) and by increasing the r_k of the detection cells in transects.

We compared the ratio of population estimate coefficient of error (CE: standard error of the estimate divided by the estimate) in 2009 to that of 2006 to study the effect of guided sampling on population estimate precision for wolf and caribou (WebTable 11). Although the population estimates were statistically indistinguishable between the years 2006 and 2009, wolf detection probabilities

increased by 20% in 2009 and there was a 26% reduction in CE. Caribou population estimates also remained statistically indistinguishable between 2006 and 2009, while caribou detection probabilities more than doubled and the CE declined by 71%. RSPF-guided sampling was not conducted for moose. Their detection probability was unchanged between 2006 and 2009, although the 2009 CE increased slightly (8%). The lack of decrease in moose CE supports our contention that the improvements in precision that we see for wolf and caribou estimates is not due to a general increase in the ability of the dog teams to detect scat, but results from guiding sampling by the RSPF for these two target species.

The dramatic reduction in CE for caribou, from 0.26 in 2006 to 0.075 in 2009, could have been caused by another factor in addition to the increased detection probability from RSPF-guided sampling: improved laboratory procedures led to increased DNA amplification success in 2009 (WebTable 2), also increasing detection probability. We assessed the relative contributions of these changes to the substantial reduction in CE observed in 2009, also determining if some other explanation should be sought.

In 2009 the best model was $\{c(t) = p(t)\}$, also known as the Otis M_t model (Otis *et al.* 1978). The asymptotic CE for this model is given as

$$CE = \left(\sqrt{\hat{N}} \left(\frac{1}{\prod_{t=1}^T (1 - p_t)} + T - 1 - \sum_{t=1}^T \frac{1}{1 - p_t} \right) \right)^{-1}$$

where T is the number of sessions and p_t is the detection probability for the t^{th} session. The detection probability is the product of the probability of locating a sample and the probability of successfully amplifying the DNA in the scat. With the same effort, 605 caribou samples were located in 2006 and 803 in 2009. Thus, 2006 location probability for caribou was 78% of that in 2009. Following improvements in laboratory techniques, amplification success increased from 42% in 2006 to 90% in 2009, meaning amplification success in 2006 was 47% of that in 2009.

The CE improvements resulting from RSPF-guided sampling and increased amplification success in 2009 can be approximated by determining how effects comparable to the 2006 deficits in location probability and amplification success would impact 2009 estimated detection probabilities. Applying the 2006 location reduction alone leads to an increase in CE to 0.09. Applying the amplification reduction alone increases the CE to 0.17. These effects are neither quite additive nor multiplicative. Applying both changes produces a new CE of 0.22. This is a little less than the observed CE of 0.26 for 2006, but the CE as given above also depends on the estimated population size. Substituting in the \hat{N} for 2006, along with the two other reductions, we predict a CE of 0.29. These rough calculations indicate that the substantial reduction in CE from 2006 to 2009 is commensurate with changes expected from the identified factors. The bulk of the increase in precision came from the improvements in DNA extraction, but a substantial increase can be attributed to RSPF-guided sampling.

WebTable 1. Microsatellite loci examined for caribou, wolf, and moose

| Species | Microsatellite locus | Number of alleles observed | Observed heterozygosity | Expected heterozygosity | Polymorphic information content |
|---------|----------------------|----------------------------|-------------------------|-------------------------|---------------------------------|
| Caribou | RT1 | 9 | 0.773 | 0.712 | 0.669 |
| | RT5 | 10 | 0.899 | 0.805 | 0.775 |
| | RT7 | 12 | 0.824 | 0.799 | 0.767 |
| | RT9 | 12 | 0.937 | 0.860 | 0.843 |
| | BM4513 | 14 | 0.791 | 0.790 | 0.764 |
| | BM6506 | 10 | 0.823 | 0.808 | 0.778 |
| Wolf | 173 | 8 | 0.798 | 0.737 | 0.689 |
| | 251 | 8 | 0.738 | 0.753 | 0.712 |
| | 377 | 8 | 0.820 | 0.797 | 0.766 |
| | 671 | 7 | 0.486 | 0.502 | 0.427 |
| | 781 | 7 | 0.812 | 0.794 | 0.760 |
| | CPH5 | 6 | 0.826 | 0.711 | 0.657 |
| Moose | RT9 | 9 | 0.642 | 0.677 | 0.645 |
| | BM203 | 6 | 0.752 | 0.706 | 0.650 |
| | BM4513 | 10 | 0.763 | 0.720 | 0.675 |
| | RT5 | 4 | 0.436 | 0.468 | 0.427 |
| | RT30 | 9 | 0.815 | 0.839 | 0.818 |
| | BL42 | 18 | 0.874 | 0.885 | 0.873 |

WebTable 2. Sample quality and CERVUS results for caribou, wolf, and moose in 2006 and 2009

| Species | Year | # unique individuals genotyped | Summed P_{ID} | Probability of no match errors in dataset | Probability of no more than 1 match error | # matches with sufficient data in CERVUS | % samples amplified at ≥ 3 loci | Mean # loci matched |
|---------|------|--------------------------------|-----------------|---|---|--|--------------------------------------|---------------------|
| Caribou | 2006 | 46 | 0.073 | 0.930 | 0.997 | 47 | 42 | 3.7 |
| Caribou | 2009 | 208 | 0.019 | 0.981 | 1.0 | 354 | 90 | 5.6 |
| Wolf | 2006 | 36 | 0.043 | 0.958 | 0.999 | 39 | 85 | 5.0 |
| Wolf | 2009 | 69 | 0.044 | 0.957 | 0.999 | 55 | 79 | 4.2 |
| Moose | 2006 | 206 | 0.223 | 0.800 | 0.979 | 213 | 86 | 5.0 |
| Moose | 2009 | 160 | 0.066 | 0.936 | 0.998 | 360 | 95 | 5.6 |

WebTable 3. Labels and definitions for resource selection covariates considered in both the Base and Full RSPF models for caribou and moose

| Model | Covariate | Definition |
|------------|-----------------|--|
| Base model | Wetland | Discrete variable for wetland ecosystems as defined by the Alberta Wetland Inventory (Halsey <i>et al.</i> 2003). Within our study area, wetlands predominantly included forested black spruce (<i>Picea mariana</i>) and black spruce–tamarack (<i>Larix laricina</i>) bogs and fens. |
| Base model | Terrain | Terrain complexity: a measure of the variance in elevation within a 150-m radial distance of a site. The variance was then standardized across the study area to scale values between -1 (low terrain complexity) and >1 (high terrain complexity). |
| Base model | BLKSPR | Density of black spruce tree cover adapted from Alberta Vegetation Inventory (Alberta Sustainable Resource Development 2005) data. A density of 1.0 is approximately 100% black spruce tree cover and a density of 0 contains no or few black spruce trees. |
| Base model | Pine | Discrete variable – open stands of jack pine (<i>Pinus banksiana</i>) found on rapidly drained sandy soils typically carpeted with terrestrial reindeer lichens. Classification was derived from Alberta Vegetation Inventory data and adjusted using vegetation ground plots. Reindeer lichens are important winter caribou forage. |
| Base model | Conifer | Density of all coniferous tree cover adapted from Alberta Vegetation Inventory data (note: considered instead of Pine and BLKSPR). A density of 1.0 is approximately 100% coniferous tree cover and a density of 0 contains no or few coniferous trees. |
| Base model | Riparian | Discrete variable – sites within 100 m of streams and lakes. |
| Base model | Wildfire | Discrete variable for wildfires that have burned within the previous 40 years. |
| Base model | Shrub | Discrete variable for sites having greater than 20% ground cover of shrubs, greater than 1-m tall. Classification was derived from Alberta Vegetation Inventory data and adjusted using vegetation ground plots. |
| Base model | LF | Discrete variable for linear features (LF) associated with no or unknown levels of human use. Linear features included transmission lines, cut lines, seismic lines, power lines, and roads. |
| Base model | LFD | Distance (kilometers) to the nearest linear features (LF) associated with no or unknown levels of human use. |
| Base model | LF250 | Discrete variable for locations within 250 m of linear features (LF). |
| Base model | Primary RD | Distance (kilometers) to the nearest paved highway. Paved highways include Provincial Highway 63 and 881, which surround the study area and are associated with high traffic volumes year round. |
| Full model | Secondary RD | Distance (kilometers) to main winter roads that provide access to oil field exploration camps and facilities. These roads included both all-season gravel access roads and winter ice roads. Traffic monitors at several secondary road locations found volumes to typically exceed 40 vehicles per day across the winter season. |
| Full model | Tertiary RD | Distance (kilometers) to winter roads providing access to remote work and exploration sites. Tertiary access roads are not navigable by truck outside of frozen winter season. Tertiary roads provide access to spatially distinct regions from that of primary and secondary roads and were thus also associated with lower traffic volumes during the sampling sessions. |
| Full model | Secondary RD250 | Discrete variable for locations within 250 m of secondary roads. |
| Full model | Tertiary RD250 | Discrete variable for locations within 250 m of tertiary roads. |

WebTable 4. SIC differences for various caribou and moose resource selection models

| <i>Caribou models</i> | <i>Logistic RSPF</i> | <i>Exponential RSF</i> |
|--|----------------------|------------------------|
| LFD | -443.73 | -436.67 |
| Primary RD | -304.27 | -320.32 |
| Terrain | -178.25 | -171.19 |
| Terrain + LFD | -183.73 | -176.67 |
| Terrain + LF | -178.14 | -171.07 |
| Terrain + Wetland | -140.18 | -133.12 |
| Terrain + Primary RD | -92.19 | -85.13 |
| Terrain + Primary RD + LF | -87.86 | -84.53 |
| Terrain + Primary RD + Wetland | -52.96 | -45.89 |
| Terrain + Primary RD + Wetland + LF250 | -59.60 | -52.54 |
| Terrain + Primary RD + Wetland + LFD | -59.01 | -51.95 |
| Terrain + Primary RD + Wetland + LF | -24.42 | -17.97 |
| Terrain + Primary RD + Wetland + LF + Pine | -94.77 | -87.71 |
| Terrain + Primary RD + Wetland + LF + Wetland + BLKSPR | -17.14 | -14.07 |
| Terrain + Primary RD + Wetland + LF + BLKSPR + Wetland*BLKSPR | -6.03 | -11.47 |
| Terrain + Primary RD + Wetland + LF + BLKSPR + Wetland*BLKSPR + Fire | -9.07 | -17.66 |
| Terrain + Primary RD + Wetland + LF + BLKSPR + Wetland*BLKSPR + Pine + Fire | -5.42 | -21.39 |
| Terrain + Primary RD + Wetland + LF + BLKSPR + Wetland*BLKSPR + Pine | 0.00* | -15.05 |
| Terrain + Primary RD + Wetland + LF + BLKSPR + Wetland*BLKSPR + Pine + Secondary RD250 | -7.85 | -21.39 |
| Terrain + Primary RD + Wetland + LF + BLKSPR + Wetland*BLKSPR + Pine + Secondary RD250 + Tertiary RD250 | -13.61 | -27.40 |
| Terrain + Primary RD + Wetland + LF + BLKSPR + Wetland*BLKSPR + Pine + Secondary RD | +13.44 | -11.54 |
| Terrain + Primary RD + Wetland + LF + BLKSPR + Wetland*BLKSPR + Pine + Secondary RD + Tertiary RD | +20.4** | -5.9 |
| <i>Moose models</i> | | |
| Conifer | -197.86 | -191.15 |
| Primary RD | -358.81 | -368.70 |
| Conifer + Fire | -149.43 | -145.69 |
| Conifer + Primary RD | -138.26 | -132.29 |
| Conifer + Primary RD + Fire | -83.94 | -77.23 |
| Conifer + Primary RD + Fire + Primary RD*Fire | -41.61 | -43.49 |
| Conifer + Primary RD + Fire + Primary RD*Fire + Shrub | -16.09 | -25.84 |
| Conifer + Primary RD + Fire + Primary RD*Fire + Riparian | -12.83 | -30.76 |
| Conifer + Primary RD + Fire + Primary RD*Fire + Shrub + Riparian | -1.70 | -20.25 |
| Conifer + Primary RD + Fire + Primary RD*Fire + Shrub + Riparian + LFD | -7.98 | -26.94 |
| Conifer + Primary RD + Fire + Primary RD*Fire + Shrub + Riparian + LF250 | -6.79 | -25.55 |
| Conifer + Primary RD + Fire + Primary RD*Fire + Shrub + Riparian + LF | 0.00* | -11.86 |
| Conifer + Primary RD + Fire + Primary RD*Fire + Shrub + Riparian + LF + Secondary RD | -0.53 | -12.06 |
| Conifer + Primary RD + Fire + Primary RD*Fire + Shrub + Riparian + LF + Secondary RD + Tertiary RD | -6.50 | -16.83 |
| Conifer + Primary RD + Fire + Primary RD*Fire + Shrub + Riparian + LF + Secondary RD250 | +10.92 | -3.35 |
| Conifer + Primary RD + Fire + Primary RD*Fire + Shrub + Riparian + LF + Secondary RD250 + Tertiary RD250 | +20.08** | +3.22 |

Notes: SIC difference for each candidate model was calculated from the best-fit base model for each of species. A model with a larger SIC difference value is considered to provide a better fit. Covariates for each model are presented in the order of relative importance (highest to lowest). See WebTable 3 for abbreviation definitions. *Best-fit basal model based on SIC; **best-fit full model based on SIC.

WebTable 5. Parameter estimates and standard errors in the final caribou and moose resource selection models

| Covariates | Parameter estimate | Standard error |
|---------------------------|--------------------|----------------|
| Caribou base model | | |
| Intercept | -3.70 | 0.30 |
| Terrain | -0.93 | 0.13 |
| Primary RD | 0.11 | 0.02 |
| Wetland | 2.11 | 0.31 |
| LF | 2.17 | 0.44 |
| BLKSPR | 0.85 | 0.51 |
| Wetland*BLKSPR | -3.14 | 0.75 |
| Pine | 1.01 | 0.33 |
| Caribou full model | | |
| Intercept | -5.60 | 0.57 |
| Terrain | -0.93 | 0.14 |
| Primary RD | 0.16 | 0.02 |
| Wetland | 1.99 | 0.27 |
| LF | 2.71 | 0.63 |
| BLKSPR | 0.71 | 0.53 |
| Wetland*BLKSPR | -3.23 | 0.73 |
| Pine | 0.91 | 0.34 |
| Secondary RD | 0.07 | 0.02 |
| Tertiary RD | 0.03 | 0.01 |
| Moose base model | | |
| Intercept | -1.57 | 0.30 |
| Conifer | -3.25 | 0.33 |
| Primary RD | 0.03 | 0.01 |
| Fire | -1.59 | 0.45 |
| Primary RD*Fire | 0.13 | 0.02 |
| Riparian | 0.62 | 0.17 |
| Shrub | 0.73 | 0.20 |
| LF | -0.46 | 0.16 |
| Moose full model | | |
| Intercept | -1.40 | 0.30 |
| Conifer | -3.17 | 0.32 |
| Primary RD | 0.03 | 0.01 |
| Fire | -1.95 | 0.48 |
| Primary RD*Fire | 0.15 | 0.03 |
| Riparian | 0.68 | 0.17 |
| Shrub | 0.75 | 0.20 |
| LF | -0.50 | 0.17 |
| Secondary RD250 | -3.51 | 1.25 |
| Tertiary RD250 | -2.38 | 0.70 |

Notes: Both models are in the Logistic RSPF form. Positive parameter estimates indicate a positive relationship between the covariate and resource selection.

WebTable 6. Parameter estimates and standard errors in the deer RSPF model (logistic RSPF model form)

| Covariates* | Parameter estimate | Standard error |
|-------------------------------------|--------------------|----------------|
| Intercept | -1.04 | 0.14 |
| Deciduous tree cover | 0.49 | 0.18 |
| (Deciduous tree cover) ² | -0.34 | 0.07 |
| Conifer tree cover | -1.00 | 0.07 |
| Terrain | 0.25 | 0.05 |
| Tree height | 3.49 | 0.41 |
| Conifer tree cover*tree height | 0.90 | 0.19 |

Notes: Positive parameter estimates indicate a positive relationship between the covariate and resource selection. *Each covariate standardized by mean and standard deviation.

WebTable 7. SIC differences for various wolf resource selection models

| Wolf model covariates | Logistic RSPF | Exponential RSF |
|--|---------------|-----------------|
| LF | -33.80 | -33.80 |
| Deer RSPF | -56.05 | -53.31 |
| Caribou RSPF | -61.82 | -56.97 |
| Moose RSPF | -68.53 | -80.25 |
| LF + Caribou RSPF | -10.34 | -5.14 |
| LF + Moose RSPF | -38.81 | -33.60 |
| LF + Deer RSPF | -6.05 | -1.43** |
| LF + Deer RSPF + Moose RSPF | -10.63 | -6.24 |
| LF + Deer RSPF + Caribou RSPF | -4.64 | 0.00* |
| LF + Deer RSPF + Moose RSPF + Caribou RSPF | -7.80 | -2.77 |

Notes: SIC difference for each candidate model was calculated from the best-fit model. A model with a larger SIC difference value is considered to provide a better fit. Covariates for each model are presented in the order of relative importance (highest to lowest). *Best-fit model based on SIC; **second best-fit model based on SIC.

WebTable 8. Parameter estimates and standard errors in the final wolf resource selection model

| Covariates | Parameter estimate | Standard error |
|---|--------------------|----------------|
| Final resource selection model for wolf | | |
| LF | 1.18 | 0.15 |
| Deer RSPF | 4.85 | 0.81 |
| Best fit model based on SIC (not recommended as final model because deer and caribou RSPF covariates are highly collinear) | | |
| LF | 1.20 | 0.15 |
| Deer RSPF | 3.27 | 1.00 |
| Caribou RSPF | -1.05 | 0.41 |

Notes: The final wolf model is in the exponential RSF form. Positive parameter estimates indicate a positive relationship between the covariate and resource selection.

WebTable 9. SIC scores after each new variable was added to the final general linear model to determine their effects on GC and T3 in caribou and moose

| Variable | Caribou T3 (n = 350) | Caribou GC (n = 388) | Moose T3 (n = 300) | Moose GC (n = 304) |
|-------------------------------|-------------------------|-------------------------|-----------------------|-----------------------|
| Base RSPF (bRSPF) | 11.46 | 254.0 | 187.77 | 28.11 |
| Primary roads | -23.02 | 201.37 | 186.46 | 27.88 |
| Exploration roads (eRoads) | -23.24 | 198.93 | LFD: 185.29 | 27.55 |
| Session | -41.32 | 146.64 | 21.11 | 21.15 |
| Session × bRSPF | -47.86 | 135.34 | 9.77 | 18.44 |
| Session × eRoads | -74.62 | 111.48 | | -3.46 |
| eRoads × bRSPF | -77.17 | 102.53 | | |
| eRoads × bRSPF × Session | -84.79 | | | |

Notes: n = sample size; LFD = linear feature density, instead of roads, significant for moose T3 only. A model with a smaller SIC value is considered to provide a better fit.

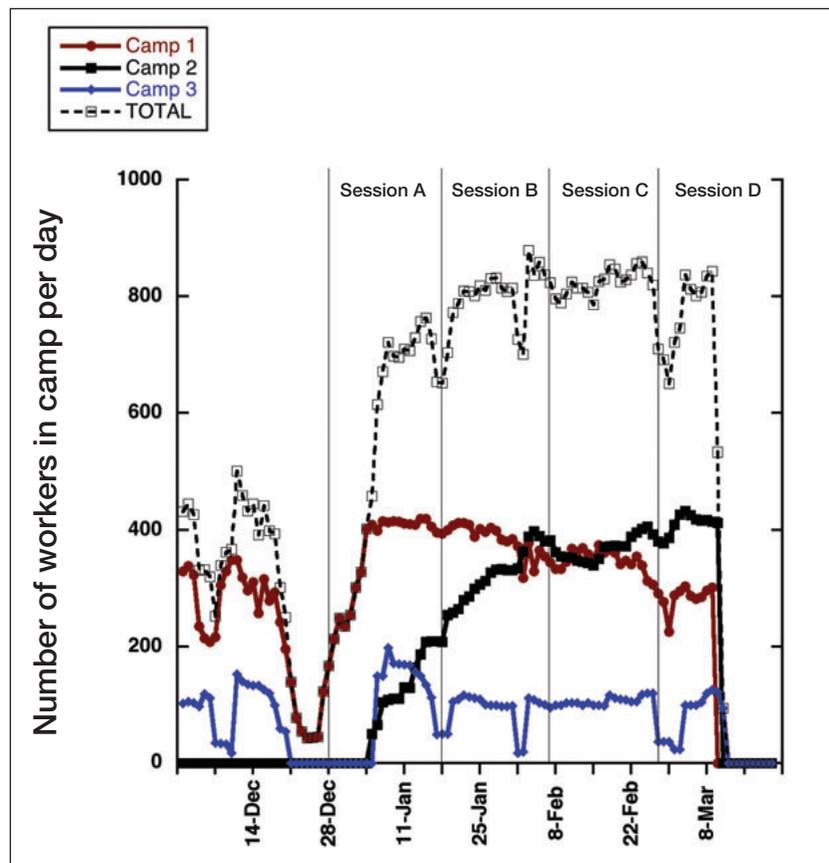
WebTable 10. Summary of mark-recapture results for caribou, wolf, and moose in 2006 and 2009

| Species | Year | Best model | Mean detection probability | Δ SIC next model | Number of parameters |
|---------|------|---------------|----------------------------------|-------------------------|-------------------------|
| Caribou | 2006 | {c(t) = p(t)} | 0.09 | 9.62 | 5 |
| Caribou | 2009 | {c(t) = p(t)} | 0.21 | 7.19 | 5 |
| Wolf | 2006 | {c(t) = p(t)} | 0.13 | 1.71 | 5 |
| Wolf | 2009 | {c(.) = p(.)} | 0.15 | 5.34 | 2 |
| Moose | 2006 | {c(.), p(.)} | 0.11 | 12.61 | 3 |
| Moose | 2009 | {c(.) = p(.)} | 0.11 | 21.55 | 2 |

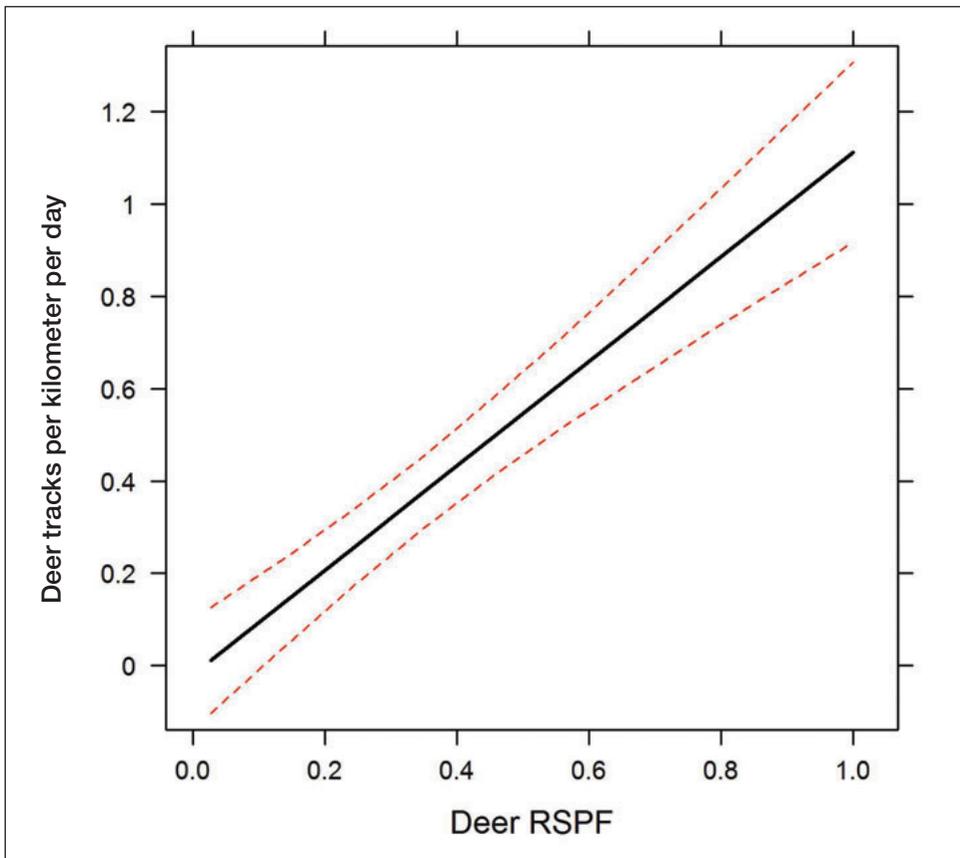
WebTable 11. Influence of RSPF-guided sampling on the precision of population estimates for wolf, caribou, and moose in 2006 and 2009

| Species | Year | RSPF- guided sampling | Lower 95% CL | MLE N estimate | Upper 95% CL | SE | CE | CE ratio 09/06 |
|---------|------|-----------------------------|--------------------|-------------------|--------------------|------|-------|----------------------|
| Wolf | 2006 | No | 57 | 85 | 155 | 23.1 | 0.27 | 0.74 |
| Wolf | 2009 | Yes | 82 | 113 | 178 | 23.0 | 0.20 | |
| Caribou | 2006 | No | 180 | 277 | 471 | 71 | 0.26 | 0.29 |
| Caribou | 2009 | Yes | 290 | 330 | 389 | 24.8 | 0.075 | |
| Moose | 2006 | No | 252 | 304 | 416 | 39.5 | 0.13 | 1.08 |
| Moose | 2009 | No | 303 | 387 | 519 | 53.9 | 0.14 | |

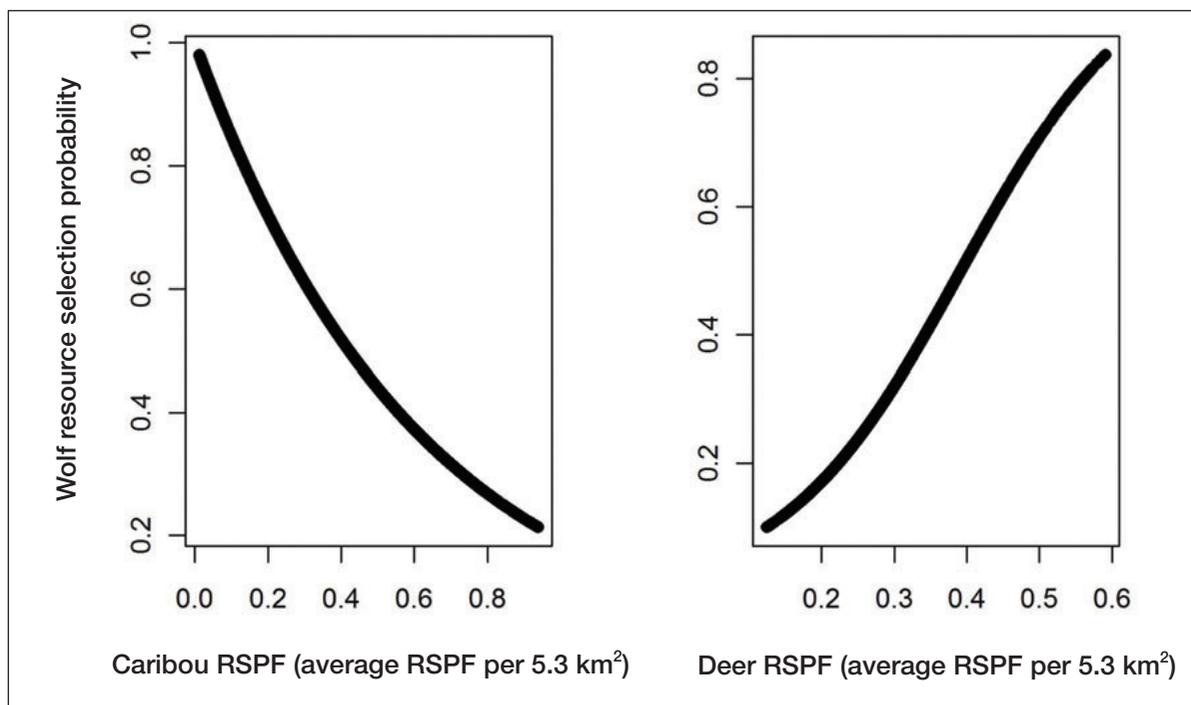
Notes: SE is the standard error of the estimate. CE is the coefficient of error (SE/estimate). The CE ratio (CE 2009/CE 2006) expresses the change in precision; a ratio less than 1 indicates that uncertainty has decreased.



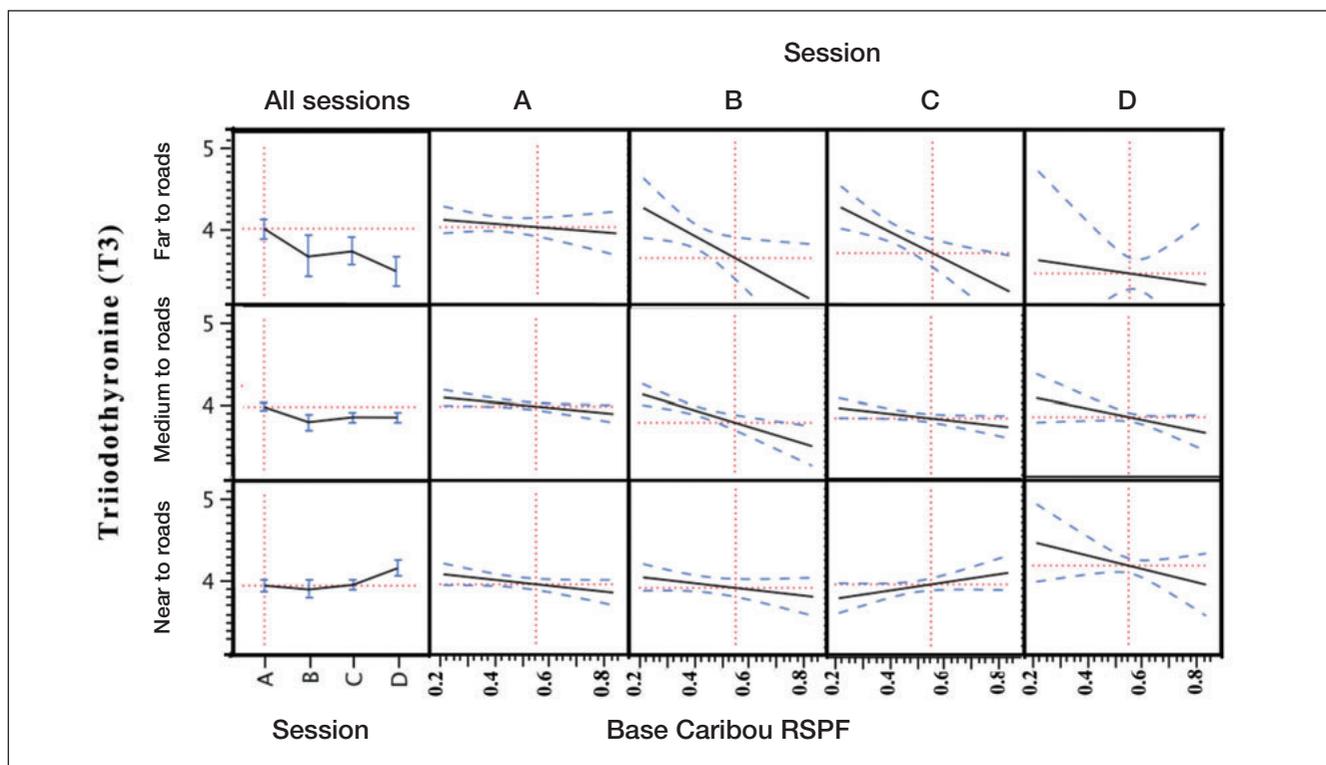
WebFigure 1. Number of oil workers in the study area staying at the various camps, plotted in relation to the four scat-dog sampling sessions.



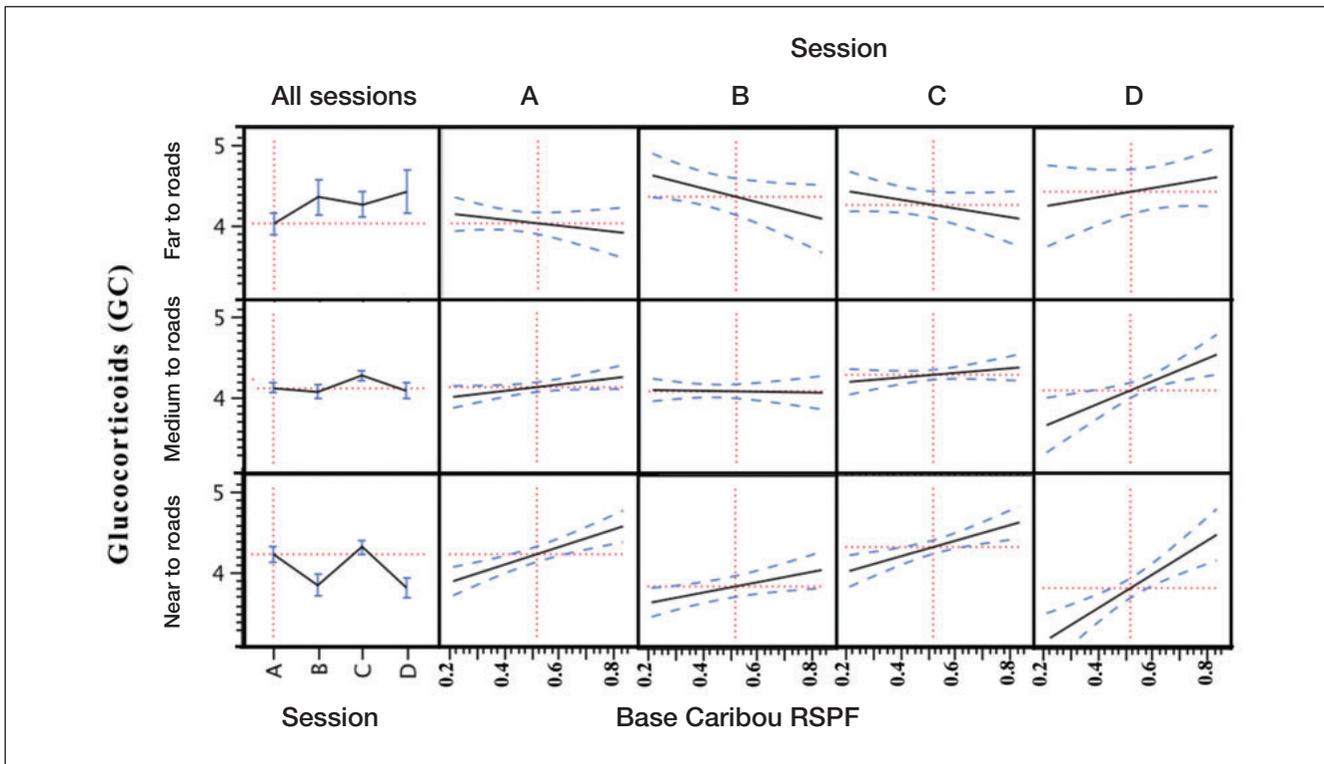
WebFigure 2. Relationship between the rates of deer tracks encountered during snow tracking sampling within the study area, and the probability of selection by deer. The rate of deer tracks encountered is corrected by the number of days since a track-obliterating snowfall. Dashed lines reflect 95% confidence intervals in the linear relationship.



WebFigure 3. Relationship between the probability of resource selection by wolves and the average RSPF of caribou and deer averaged across 5.3 km² (displaying single covariate logistic RSPF models for each species).



WebFigure 4. Interaction plot of changes in thyroid hormone (triiodothyronine, T3) concentrations with proximity to oil extraction roads during each sampling session. The left-most column shows the overall effect of sessions on T3 concentrations. The remaining columns indicate effects across sessions A–D. Effects caused by proximity to roads are indicated by row, where the top row represents effects on T3 when far from roads (>10 km), the middle row represents effects at medium distances from roads (3–10 km), and the bottom row represents effects close to roads (< 3 km). Error bars (left-most column) and dashed lines (remaining columns) indicate 95% confidence intervals.



WebFigure 5. Interaction plot of changes in glucocorticoid (GC) hormone concentrations with proximity to oil extraction roads during each sampling session. The left-most column shows the overall effect of sessions on GC concentrations. The remaining columns indicate effects across sessions A–D. Effects caused by proximity to roads are indicated by row, where the top row represents effects on GCs when far from roads (>10 km), the middle row represents effects at medium distances from roads (3–10 km), and the bottom row represents effects close to roads (< 3 km). Error bars (left-most column) and dashed lines (remaining columns) indicate 95% confidence intervals.

■ WebReferences

- Alberta Sustainable Resource Development. 2005. Alberta vegetation inventory version interpretation standards. Version 2.1.1. Edmonton, Canada: Resource Information Management Branch, Alberta Sustainable Resource Development.
- Arts G, Mackenzie ML, McConnell BJ, *et al.* 2008. Estimating space-use and habitat preferences from wildlife telemetry data. *Ecography* **31**: 140–60.
- Astrup R, Coates KD, and Hall E. 2008. Finding the appropriate level of complexity for a simulation model: an example with a forest growth model. *Forest Ecol Manag* **256**: 1659–65.
- Ball MC, Pither R, Mansey M, *et al.* 2007. Characterization of target nuclear DNA from faeces reduces technical issues associated with the assumptions of low-quality and quantity template. *Conserv Genet* **8**: 577–86.
- Dice LR. 1938. Some census methods for mammals. *J Wildlife Manage* **2**: 119–30.
- Douyon L and Schteingart DE. 2002. Effect of obesity and starvation on thyroid hormone, growth hormone, and cortisol secretion. *Endocrin Metab Clin* **31**: 173–89.
- Foran DR, Cooks KR, and Minta SC. 1997. Species identification from scat: an unambiguous genetic method. *Wildlife Soc B* **25**: 835–39.
- Halsey LA, Vitt DH, Beilman D, *et al.* 2003. Alberta Wetland Inventory Classification System Version 2.0. Edmonton, Canada: University of Alberta.
- James ARC and Stuart-Smith AK. 2000. Distribution of caribou and wolves in relation to linear corridors. *J Wildlife Manage* **64**: 154–59.
- Kalinowski ST, Taper ML, and Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol Ecol* **16**: 1099–106.
- Kalinowski ST, Sawaya MA, and Taper ML. 2006. Individual identification and distribution of genotypic differences between individuals. *J Wildlife Manage* **70**: 1148–50.
- Keim J, DeWitt P, and Lele S. Predators choose prey over prey habitats: evidence from a lynx–hare system. *Ecol Appl*; doi:10.1890/10-0949.1. In press.
- Kendall WL. 1999. Robustness of closed capture–recapture methods to violations of the closure assumption. *Ecology* **80**: 2517–25.
- Kitaysky AS, Romano MD, Piatt JF, *et al.* 2005. The adrenocortical response of tufted puffin chicks to nutritional deficits. *Horm Behav* **47**: 606–19.
- Lele SR and Keim JL. 2006. Weighted distributions and estimation of resource selection probability functions. *Ecology* **87**: 3021–28.
- Murtaugh PA. 2009. Performance of several variable-selection methods applied to real ecological data. *Ecol Lett* **12**: 1061–68.
- Otis DL, Burnham KP, White GC, and Anderson DR. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monogr* **62**: 3–135.
- Raffalovich LE, Deane GD, Armstrong D, and Tsao HS. 2008. Model selection procedures in social research: Monte-Carlo simulation results. *J Appl Stat* **35**: 1093–114.
- Schwarz G. 1978. Estimating the dimension of a model. *Ann Stat* **6**: 461–64.
- Stanley TR and Burnham KP. 1999. A closure test for time-specific capture–recapture data. *Environ Ecol Stat* **6**: 197–209.
- Stanley TR and Richards JD. 2004. CloseTest version 3.0. Fort Collins, CO: US Geological Survey.
- Taper ML. 2004. Model identification from many candidates. In: Taper ML and Lele SR (Eds). *The nature of scientific evidence: statistical, philosophical and empirical considerations*. Chicago, IL: University of Chicago Press.
- Wasser SK, Houston CS, Koehler GM, *et al.* 1997. Techniques for application of fecal DNA studies of Ursids. *Mol Ecol* **6**: 1091–97.
- Wasser SK, Monfort SL, Souther J, and Wildt DE. 1994. Excretion rates and metabolites of oestradiol and progesterone in baboon (*Papio cynocephalus*) faeces. *J Reprod Fertil* **101**: 213–20.
- Wasser SK, Shedlock A, Comstock K, *et al.* 2004. Assigning African elephant DNA to geographic region of origin: applications to the ivory trade. *P Natl Acad Sci USA* **101**: 14847–52.
- Wasser SK, Thomas R, Nair PP, *et al.* 1993. Effects of dietary fiber on faecal steroid measurements. *J Reprod Fertil* **97**: 569–74.
- Wasser SK, Hunt KE, Brown JL, *et al.* 2000. A generalized fecal glucocorticoid assay for use in a diverse array of non-domestic mammalian and avian species. *Gen Comp Endocr* **120**: 260–75.
- Wasser SK, Cristóbal-Azkarate J, Booth RK, *et al.* 2010. Non-invasive measurement of thyroid hormone in feces of diverse array of avian and mammalian species. *Gen Comp Endocr* **168**: 1–7.
- White GC. 2009. MARK version 6.1. <http://wamerncr.colostate.edu/~gwhite/mark/mark.htm#Documentation>. Viewed 11 Apr 2011.
- Wilson KR and Anderson DR. 1985. Evaluation of two density estimators of small mammal population-size. *J Mammal* **66**: 13–21.