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Evaluating Potential Effects of an Industrial Road on Winter Habitat of Caribou in North-Central Alaska

RYAN R. WILSON,[1] DAVID D. GUSTINE[2] and KYLE JOLY[3]

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ABSTRACT. Worldwide, some caribou (*Rangifer tarandus*) populations are experiencing declines due partially to the expansion of industrial development. Caribou can exhibit behavioral avoidance of development, leading to indirect habitat loss, even if the actual footprint is small. Thus, it is important to understand before construction begins how much habitat might be affected by proposed development. In northern Alaska, an industrial road that has been proposed to facilitate mining transects a portion of the Western Arctic caribou herd's winter range. To understand how winter habitat use might be affected by the road, we estimated resource selection patterns during winter for caribou in a study area surrounding the proposed road. We assessed the reductions of habitat value associated with three proposed routes at three distance thresholds for disturbance. High-value winter habitat tended to occur in locally rugged areas that have not burned recently and have a high density of lichen and early dates of spring snowmelt. We found that 1.5% to 8.5% (146–848 km^2) of existing high-value winter habitat in our study area might be reduced in quality. The three alternative routes were only marginally different. Our results suggest that the road would have minimal direct effects on high-value winter habitat; however, additional cumulative impacts to caribou (e.g., increased access by recreationists and hunters) should be considered before the full effects of the road can be estimated.

Key words: Alaska, caribou, development, *Rangifer tarandus*, resource selection, roads, winter

RÉSUMÉ. À l'échelle mondiale, certaines populations de caribous (*Rangifer tarandus*) connaissent des déclins partiellement attribuables à l'expansion industrielle. Pour des raisons de comportement, le caribou peut éviter le développement, ce qui entraîne une perte d'habitat indirecte, et ce, même si la place réellement occupée est petite. Par conséquent, il est important de comprendre, avant même que des travaux de construction ne soient amorcés, dans quelle mesure l'habitat sera touché par les travaux proposés. Dans le nord de l'Alaska, une route industrielle dont la construction a été proposée pour faciliter l'exploitation minière coupe transversalement une partie de l'aire d'hivernage du troupeau de caribous de l'ouest de l'Arctique. Afin de comprendre comment l'utilisation de l'habitat d'hivernage pourrait être touchée par la route, nous avons estimé des modèles de sélection des ressources pendant l'hiver pour le caribou se trouvant dans une aire d'étude entourant la route proposée. Nous avons évalué la diminution de la valeur de l'habitat liée à trois routes proposées à trois seuils de distance afin d'en déterminer la perturbation. Un habitat d'hivernage de grande valeur avait tendance à se manifester dans les régions locales accidentées qui n'avaient pas fait l'objet de brûlages récents, régions caractérisées par une forte densité de lichen et une fonte des neiges hâtive au printemps. Dans le cadre de notre étude, nous avons constaté que la qualité de 1,5 % à 8,5 % (146–848 km^2) de l'habitat d'hivernage actuel de grande valeur pourrait être réduite. Les trois routes différaient à peine. Nos résultats suggèrent que la route aurait des effets directs minimes sur l'habitat d'hivernage de grande valeur. Cependant, il y a lieu de considérer les incidences cumulatives supplémentaires (comme l'accès accru par les amateurs de plein air et les chasseurs) afin de pouvoir estimer les effets complets de la route.

Mots clés : Alaska, caribou, développement, *Rangifer tarandus*, sélection des ressources, routes, hiver

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INTRODUCTION

Throughout the North, some caribou (*Rangifer tarandus*) populations are experiencing declines that are due in part to the expansion of industrial development (Festa-Bianchet et al., 2011). Industrial development can affect caribou directly, through conversion of habitat to infrastructure (e.g., roads and production pads), or indirectly, through the behavioral avoidance by caribou of industrial activities and structures (e.g., vehicles, aircraft, and power lines). The amount of direct habitat lost as a result of conversion is generally a small proportion of available habitat, while behavioral avoidance (Johnson et al., 2005) can significantly reduce caribou use of otherwise high-value habitat

[1] The Wilderness Society, 705 Christensen Drive, Anchorage, Alaska 99501, USA; ryan.radford.wilson@gmail.com
[2] U.S. Geological Survey, Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA
[3] Gates of the Arctic National Park and Preserve, Arctic Inventory and Monitoring Network, 4175 Geist Road, Fairbanks, Alaska 99709, USA

(Weclaw and Hudson, 2004). For example, Nellemann et al. (2003) reported a 70% loss of undisturbed habitats over the last century due to avoidance of infrastructure (< 4 km) for Norwegian reindeer (*R. t. tarandus*). Similarly, even relatively small industrial footprints in northern Alaska could result in a reduction of more than 30% of high-value caribou calving habitat arising from avoidance by parturient females (Wilson et al., 2013).

Caribou show seasonal variation in their response to industrial development. For example, during summer, when insect harassment increases, caribou have been observed using developed areas, where insect harassment is less severe (Murphy and Curatolo, 1987). Conversely, during calving, females with calves will avoid developed areas up to 5 km (Cameron et al., 2005). In winter, avoidance of areas adjacent to roads has been found to be dependent on activity levels (Cumming and Hyer, 1998; Nellemann et al., 2001). In particular, Cumming and Hyer (1998) found that caribou used areas near an unused logging road, but avoided the area during a winter when there was logging traffic.

Disturbance-related reductions in winter habitat quality could exacerbate other demographic constraints experienced by caribou. In North America, caribou subsist primarily on lichens during winter (Klein, 1982; Russell et al., 1993; Gustine et al., 2012) and rely on nutrient reserves established during summer and fall to survive through to the following spring (Parker et al., 2009). Winter is also the period when caribou attempt to minimize energetic costs of foraging under the snowpack (Adamczewski et al., 1988) and exposure to predation (Gustine et al., 2006). Thus, winter conditions can affect nutrient reserves available for the production of calves the following spring (Adams, 2003, 2005). If road developments within a herd's winter range reduce the availability of high-value winter habitat, shift space use to less desirable areas (e.g., those with deeper snow or increased risk of predation), or increase energetic costs of movement as a result of disturbance, productivity may be affected.

With industrial development continuing to expand into caribou habitat, it is important to map current high-value caribou habitat and understand how proposed developments might affect it (Sawyer et al., 2006; Harju et al., 2011; Wilson et al., 2013). In the north-central interior of Alaska, a proposed road to facilitate mining in the Ambler Mining District would pass through a portion of the Western Arctic caribou herd's winter range (Fig. 1). Three study corridors are currently being considered for the road. The goal of this study was to evaluate the potential effects of a road in each of these corridors on the winter habitat of the Western Arctic caribou herd.

STUDY AREA

The Western Arctic caribou herd is the largest herd in Alaska (~325 000 in 2011) and ranges over an area of 363 000 km^2 in the northwestern portion of the state (Dau, 2011). More than 40 communities in the region rely on the Western Arctic herd for their subsistence and cultural heritage. Although the mechanisms are uncertain, recent aerial surveys suggest that the herd is declining after reaching historically high population levels (Dau, 2011). Many factors may contribute to changes in caribou populations, but changes in habitat quality and availability have the greatest potential to influence the distribution and abundance of migratory tundra-dwelling caribou, particularly for herds reaching high population levels or densities (Bergerud et al., 2008).

We defined the study area within a rectangle with sides 15 km from the northern, eastern, southern, and western extents of the proposed road routes (33 175 km^2; Fig. 1) because previous studies have shown disturbance effects on caribou up to 15 km from industrial activities (Boulanger et al., 2012). The Ambler Mining District is located in north-central Alaska, just south of the Brooks Mountain Range. The proposed road corridor runs from the Dalton Highway near Bettles to Ambler, Alaska (Fig. 1). There is currently no road connecting the mining district to the primary road network in the state. We considered three study corridors (DOWL HKM, 2011) for a road from the Dalton Highway to the Ambler River (Fig. 1): Northern (~ 318 km), Southern (~ 344 km), and Alatna Hills (~ 314 km).

The region consists of boreal forest in the lowlands, dominated by black spruce (*Picea mariana*) with lichen understory and paper birch (*Betula papyrifera*), interspersed with extensive wetland and riparian complexes. Tundra communities characterized by sedges (*Carex* and *Eriophorum* spp.), dwarf birch (*Betula* spp.), willow (*Salix* spp.), and bryophtyes are prevalent in areas underlain with permafrost. At higher elevations, boreal forests transition into subalpine shrublands, with alder (*Alnus* spp.), dwarf birch, willow, and alpine tundra, consisting of various low-lying willows, lichens, graminoids, *Vaccinium* spp., and *Dryas* spp. Mountain peaks are largely devoid of vegetation. Average annual temperature is −5˚C, with lows in winter below −40˚C and highs in summer more than 20˚C. Mean annual snowfall is less than 120 cm, and snow cover lasts from October to May (NCDC, 2013).

METHODS

Animal Capture and Handling

During September of each year (2009–12), we captured adult female caribou (39 in 2009, 15 in 2010, 14 in 2011, and 12 in 2012) as they swam across the Kobuk River at Onion Portage and instrumented each with a global positioning system satellite telemetry collar (Telonics TGW-4680, Mesa, Arizona, USA) (Joly, 2011). We programmed collars to acquire locations every eight hours. All animal handling was approved by the Animal Care and Use Committee of the Alaska Department of Fish and Game.

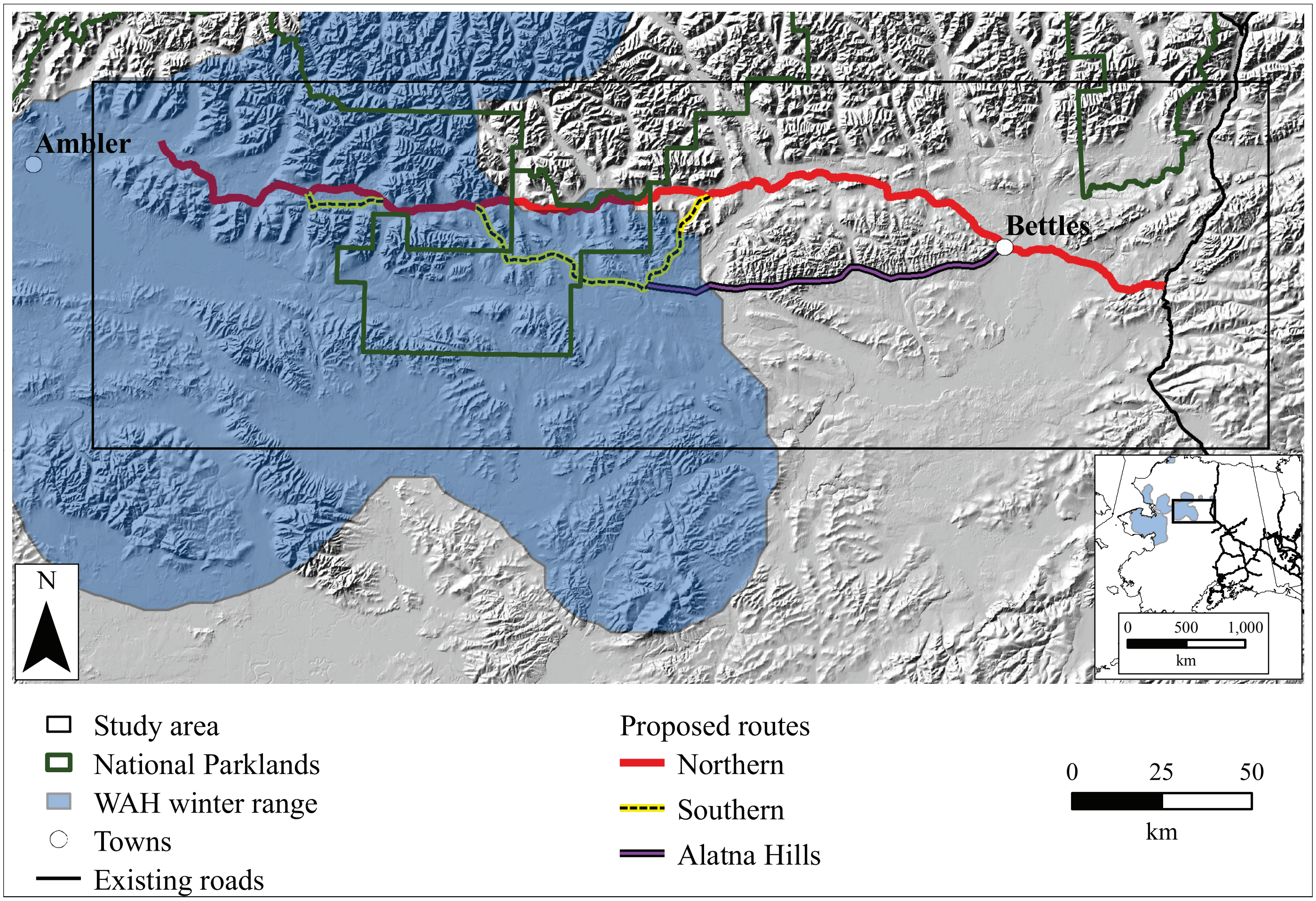

FIG. 1. Map showing the three corridors proposed for a road to connect the existing road network to the Ambler Mining District in northwestern Alaska in relation to the winter distribution of the Western Arctic caribou herd (WAH) in 1999–2005 reported by Joly et al. (2007).

Habitat Variables

The occurrence of lichens in caribou diets during winter has been regularly documented (Russell et al., 1993; Gustine et al., 2012). Thus, we created a data layer for the presence and absence of lichen across the study area based on the vegetation map developed by Boggs et al. (2012). We classified any pixel as having lichen presence if the vegetation classification for that pixel listed lichens as a dominant species of ground cover. We used the same vegetation map to create a map of the presence or absence in the study area of dense vegetation (e.g., riparian, tall shrub, and forested areas), which caribou typically avoid because of predation risk or lack of winter forage (Joly et al., 2010).

Fire has been documented as an important factor influencing lichen production (Collins et al., 2011) and the winter distribution of caribou (Joly et al., 2007, 2010), so we included a covariate for the number of years since a fire occurred across the study area (AICC, 2013). During winter, caribou in this herd avoided burns that were less than 60 years old (Joly et al., 2010); therefore, for pixels without a fire recorded since the 1940s, we set the number of years since a burn to 60 years.

We also included a variety of topographic variables into the set available for model selection, given their previously documented importance in other resource selection studies for caribou (Gustine et al., 2006; Joly et al., 2011). We used a digital elevation model (60 m; Gesch, 2007) to obtain elevation data. We then used these data to calculate percent slope and terrain ruggedness. We used the vector ruggedness measure developed by Sappington et al. (2007) at two scales (180 m and 1020 m) to calculate terrain ruggedness. Finally, because the energetic cost of movement increases with increasing snow depth (Fancy and White, 1987), we included a measure of the mean snow-free date for each pixel (30 m) in the study area as an index of snow depth, using Landsat-derived data from 1985 to 2011 (Macander and Swingley, 2012).

We tested for collinearity between explanatory variables by calculating variance inflation factors with the “corvif” function in the AED library in R (Zuur et al., 2009). We excluded the variable with the highest value greater than three, and then recalculated the variance inflation factors for all remaining variables. We continued this process until all remaining variables had variance inflation values less than three; this criterion excluded the large-scale (i.e., 1020 m) index of terrain ruggedness.

Data Analysis

Recent (1999–2005; Joly et al., 2007) and current distributions of the Western Arctic caribou herd (Joly et al., 2010; Dau, 2011) suggest caribou will most likely encounter the proposed routes in winter. Thus, we restricted our analyses to the winter season. Rather than define a winter season by arbitrary start and end dates, we chose to use individual movement patterns to define the period when each individual was on its winter range. We estimated net-squared displacement for each individual from 1 July of each year to 30 June of the next and used the inflection points of these data to identify the start and end dates of both spring and fall migration (Bunnefeld et al., 2011). We defined winter for each individual as the period between the end of fall migration and the beginning of spring migration. We were unable to estimate the dates of fall migration for the year an individual was captured. In these cases (n = 8), we defined winter as occurring between 1 January and the start of spring migration the following year, since all individuals were on winter ranges by 1 January.

Estimates of resource selection (and their interpretation) are sensitive to the scale at which selection is measured (Beyer et al., 2010). Thus, particular attention must be paid to which scale of selection best addresses the desired question. In this study, we were interested in how caribou movement on their winter range might be affected by a road, so we estimated resource selection at the scale of individual steps. While this scale is not able to estimate larger-scale avoidance of the area by the Western Arctic caribou herd, our primary interest was in how space-use patterns might be affected for caribou that winter in the area adjacent to the road. To model resource selection, we used a step selection approach implemented with conditional logistic regression following the methods of Forester et al. (2009). The step selection model took the general form:

$$g_u(s,t) = \frac{g_a(s,t) \times w(s)}{\int g_a(s,t) \times w(s) ds}$$

where $g_u(s,t)$ is the probability of use at location s at time t, $g_a(s,t)$ is the probability of using location s at time t in the absence of resource selection (i.e., availability), and $w(s)$ is the selection function describing habitat preferences that transforms $g_a(s,t)$ to $g_u(s,t)$ by selectively weighting different areas on the basis of underlying landscape attributes at location s. We defined the selection function as:

$$w(s) = Exp[\beta' X(s)]$$

where β is a vector of selection coefficients to be estimated and $X(s)$ is a vector of habitat covariates measured at location s. To approximate $g_a(s,t)$, we obtained empirical distributions of step length and turn angle for the population of used points. For each used point, we simulated the end points of 25 random steps radiating out from the previous used location by drawing 25 samples from the step length and turn angle distributions. We built models with all combinations of variables. We included squared terms for slope and terrain ruggedness to account for the potentially non-linear responses to these variables. A bimodal pattern in the elevations of used points indicated two distinct wintering patterns within the study area. Therefore, for the full model, we interacted all of the above variables (with the exception of years since an area burned) with elevation to capture the potential for distinct patterns of selection with changes in elevation (Fig. 2). We also included the distance between the previously used location and the next used location and its associated random locations to control for bias in selection estimates (Forester et al., 2009). We scaled all variables to aid in model convergence (Zuur et al., 2009).

We used the "coxph" function in the survival package (Therneau, 2013) for R (R Development Core Team, 2012) to estimate step-selection functions, with each set of random and observed points assigned a unique cluster identity. We also used the robust variance estimator in "coxph" to help control for multiple observations per individual. We selected as the best model in our set of candidate models the one with the lowest Akaike's Information Criterion (AIC) score (Burnham and Anderson, 2002). If multiple models had a $\Delta AIC \leq 2$, we averaged models (Burnham and Anderson, 2002) to obtain the final model. We determined the predictive capacity of the final averaged model by performing k-fold cross-validation following the methods described in Fortin et al. (2009).

Evaluating Effects of the Proposed Road

To determine what effect a road through each of the three study corridors might have on caribou winter habitat, we developed a predictive map (60 m) of relative habitat value based on the final averaged model. From the predicted values, we obtained quantiles at 10% intervals and binned each pixel into ten bins. Similar to Polfus et al. (2011), we defined high-value habitat to be those pixels occurring in the top three quantiles (i.e., 70%–100% quantiles). Because we do not know what influence pixels of high-value habitat might have on an individual's fitness, our definition of high-value habitat is only related to the relative probability of a caribou using that area (i.e., the probability of selection; Lele et al., 2013). We assume, however, that if a site has a high relative probability of use, then caribou view it as having important attributes related to enhancing their fitness.

Because very few roads exist in northern Alaska, and none are currently present in the study area, we were unable to estimate a response to roads by caribou in this study. We therefore relied on estimates of disturbance distances derived from previous studies. Different studies, however, show different responses by caribou to different seasons

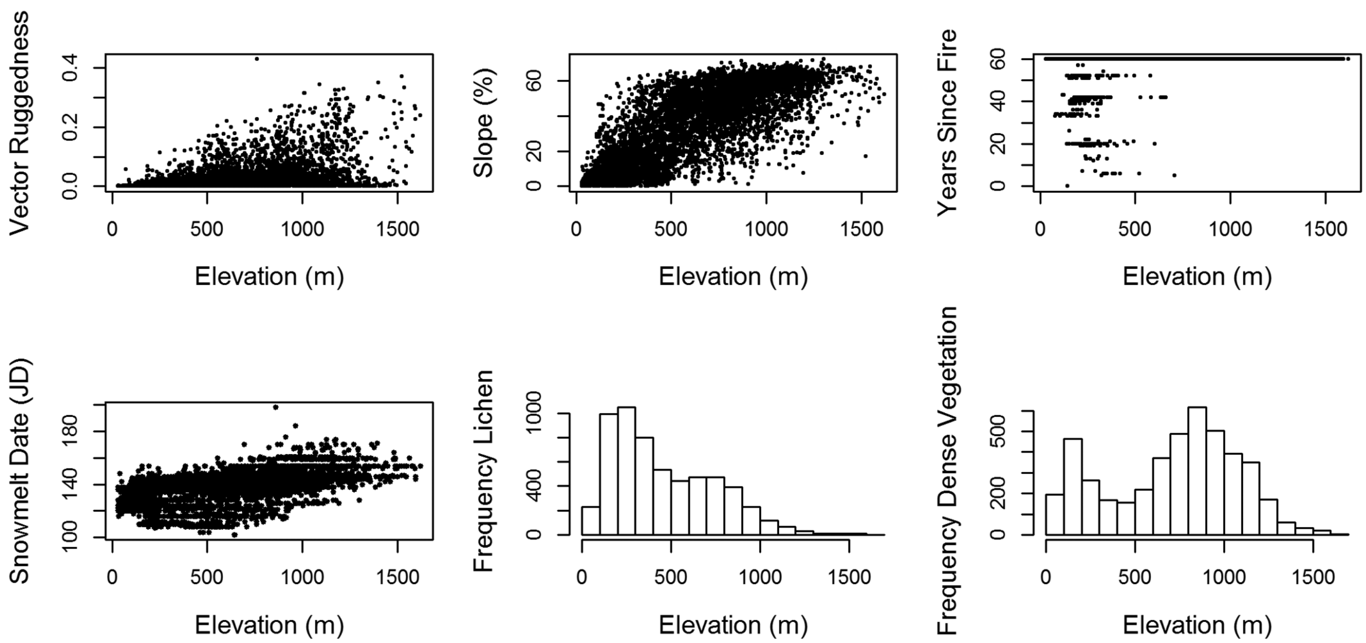

FIG. 2. Scatter plots against elevation for all variables used in models except presence of lichen and dense vegetation. Presence of lichen and dense vegetation is represented by frequency histograms of the elevations at which each vegetation type occurred.

(Wilson et al., 2012) and types of infrastructure (Nellemann et al., 2001). Additionally, the methods used to estimate disturbance (Ficetola and Denoël, 2009) and the scale at which studies occur (Vistnes and Nellemann, 2008) can influence estimates and their interpretation. Because of the above issues and the uncertainty of how caribou in our study area might respond to a road through their wintering area, we used a range of disturbance distances obtained from previous studies on wintering caribou (e.g., Cumming and Hyer, 1998; Nellemann et al., 2001; Polfus et al., 2011). Estimates on how far caribou avoid roads during winter range from 1 km (e.g., Polfus et al., 2011) to 5 km (Cumming and Hyer, 1998; Nellemann et al., 2001). Thus, we assessed the potential effects of a road through each study corridor on winter habitat from three assumed disturbance distances: 1 km, 2.5 km, and 5 km. It is possible that caribou could be disturbed at distances greater than 5 km during winter, but we wanted to be cautious in applying disturbance distances beyond those that have been documented in the literature, especially given that we have limited data on caribou responses to roads during winter in northern Alaska. Our results might therefore prove to be biased low if future studies show larger winter disturbance distances associated with industrial roads.

As road locations have not yet been determined for each study corridor, we used the centerline of each corridor to derive the above distances (DOWL HKM, 2011). Other studies have found non-linear responses to infrastructure (e.g., Cameron et al., 2005; Johnson et al., 2005); however, none of the studies of winter disturbance provided sufficient data to estimate a disturbance curve. Therefore, we relied on a simple linear reduction of disturbance as a function of distance to the road. For each disturbance distance, we discounted a pixel's (60 m) value on the basis of its distance from the study corridor's centerline and the maximum distance at which the disturbance effect was assumed to occur. For example, if a pixel occurred 4 km from a study corridor's centerline, and caribou were assumed to exhibit disturbance outwards to 5 km from a road, the original predicted value of that pixel would be reduced by 20% (i.e., [5 km − 4 km]/5 km). After this calculation was completed for all pixels, we summed the number of pixels that remained classified as high-value habitat and compared that sum to the original number of high-value pixels in the study area. We do not believe that our results would differ substantially if the actual location of the road differed from the centerline of the corridor given that the road would still occur in a region with similar landscape attributes. Even so, these modeled results should be interpreted as relative differences between study corridors and not absolute differences in the amount of high-value habitat affected.

RESULTS

Of the 80 individuals initially captured, 24 spent at least a portion of one winter in the study area (range, 40–217 days), and four individuals spent a portion of two winters in there. The number of individuals that were active in the study area varied among years (i.e., 2009–10 = 4, 2010–11 = 15, 2011–12 = 8, and 2012–13 = 1), as did the number of relocations obtained each winter (i.e., 2009–10 = 365, 2010–11 = 5655, 2011–12 = 1956, and 2012–13 = 22); the percentage of all winter locations occurring inside the study area (i.e., 2009–10 = 3.1%, 2010–11 = 28.0%, 2011–12 = 9.0%, and 2012–13 = 0.2%); and the average (± SD) number of

TABLE 1. List of competing models (ΔAIC ≤ 2) of winter resource selection patterns for the Western Arctic caribou herd in the area of the proposed road to the Ambler Mining District, Alaska. If a squared term is present, then the non-squared term is also present in the model. All models included a term for distance to used and random points from the previous used point but this term is not listed in the models below.

Model[1]	ΔAIC	k
DenseVeg+Slope^2+Snow+Rugged^2+Fire+Lichen+Elev+Slope^2*Elev	0.00	12
DenseVeg+ Slope^2+Snow+Rugged^2+Elev+Slope^2*Elev+Rugged*Elev	0.30	13
DenseVeg+Slope^2+Snow+Rugged^2+Fire+Lichen+Elev+DenseVeg*Elev+Slope*Elev+Slope^2*Elev	0.90	13
DenseVeg+Slope^2+Snow+Rugged^2+Fire+Lichen+Elev+Lichen*Elev+Slope*Elev+Slope^2*Elev	1.00	13
DenseVeg+Slope^2+Snow+Rugged^2+Fire+Lichen+Elev+Lichen*Elev+Slope^2*Elev+Rugged*Elev	1.10	14
DenseVeg+Slope^2+Snow+Rugged^2+Lichen+Elev+DenseVeg*Elev+Slope^2*Elev+Rugged*Elev	1.40	14
DenseVeg+Slope^2+Snow+Rugged^2+Fire+Lichen+Elev+DenseVeg*Elev+Lichen*Elev+Slope^2*Elev	1.70	14
DenseVeg+Slope^2+Snow+Rugged^2+Fire+Lichen+Elev+Slope^2*Elev+Snow*Elev	2.00	13

[1] DenseVeg = dense vegetation, Fire = years since fire, Elev = elevation, Snow = date of snowmelt, and Rugged = the vector ruggedness measure.

TABLE 2. Parameters and coefficients for the final averaged model used to estimate winter resource selection patterns for the Western Arctic caribou herd in the area of the proposed road to the Ambler Mining District, Alaska, 2009–12.

Parameter	Coefficient	SE
DenseVeg	−0.153	0.053
Slope	−0.260	0.052
Slope^2	−0.105	0.051
Snowmelt date	−0.234	0.035
Ruggedness	0.049[a]	0.048
Ruggedness^2	−0.013[a]	0.011
Years since fire	0.141	0.020
Lichen	0.099[a]	0.064
Elevation	0.383	0.125
Elevation*Slope	0.273	0.049
Elevation*Slope^2	−0.116	0.038
Elevation*Ruggedness	0.022[a]	0.023
Elevation*Dense vegetation	−0.040[a]	0.066
Elevation*Lichen	−0.044[a]	0.062
Elevation*Snowmelt date	−0.0002[a]	0.034
Distance	−0.00003	< 0.001

[a] Indicates that the 95% confidence interval overlaps 0.

days individuals spent in the study area each winter (i.e., 2009–10 = 58 ± 35, 2010–11 = 152 ± 61, 2011–12 = 102 ± 66, 2012–13 = 7 [no SD estimate]).

Resource Selection

We obtained eight competing models (i.e., ΔAIC ≤ 2; Table 1), so our final model was a weighted average of all eight (Table 2). The final model performed well in the k-fold cross validation (mean r_s = 0.936, SD = 0.031). There was a clear difference in resource selection patterns between sites at low and high elevations (Fig. 2; Table 2). At all elevations, caribou tended to select more rugged areas with steeper slopes, but the effect was stronger at higher elevations (Table 2). Additionally, caribou selected areas that had earlier snow-free dates in the spring, although caribou at higher elevations selected areas with slightly later snow-free dates (Table 2). Across the landscape, caribou selected for areas with relatively less dense vegetation, more lichen, and longer periods since fire, although the strength of these effects decreased with elevation (Table 2).

We identified 9950 km^2 of high-value habitat in the study area prior to the application of any discount associated with the roads. High-value habitat was distributed across the landscape, but was primarily located in valley bottoms within the western section of the study area and along ridgelines across its northern section (Fig. 3). It appears that a large part of the eastern portion of the study area may have once supported extensive high-value winter habitat, but recent fires have reduced the value of this area (Fig. 3). High-value habitat along the Northern route within Gates of the Arctic National Park and Preserve was similarly affected by fire (Fig. 3).

Evaluating Effects of the Proposed Road

We observed minor differences in the amount of high-value habitat lost between potential roads through each study corridor. The Southern route consistently had a marginally larger effect on habitat than the other two routes for all disturbance distances, probably because it is slightly longer (~ 30 km). At an assumed disturbance distance of 5 km, the Southern route lost approximately 1% more high-value habitat than the other two routes (Table 3).

DISCUSSION

Understanding how wildlife will be affected by future industrial activities is a challenge for researchers and resource managers (Northrup and Wittemyer, 2013). Mapped output from our resource selection model clearly indicated that areas of high-value winter habitat for caribou were concentrated in valley bottoms and along ridgelines, particularly in the western reaches of the study area. The highest-value habitat was not equally distributed along the proposed road routes, although we did not find large differences between study corridors in potential disturbance to caribou habitat. High-value habitat was reduced by 1.5% to 8.5% across study corridors; however, it is unknown what

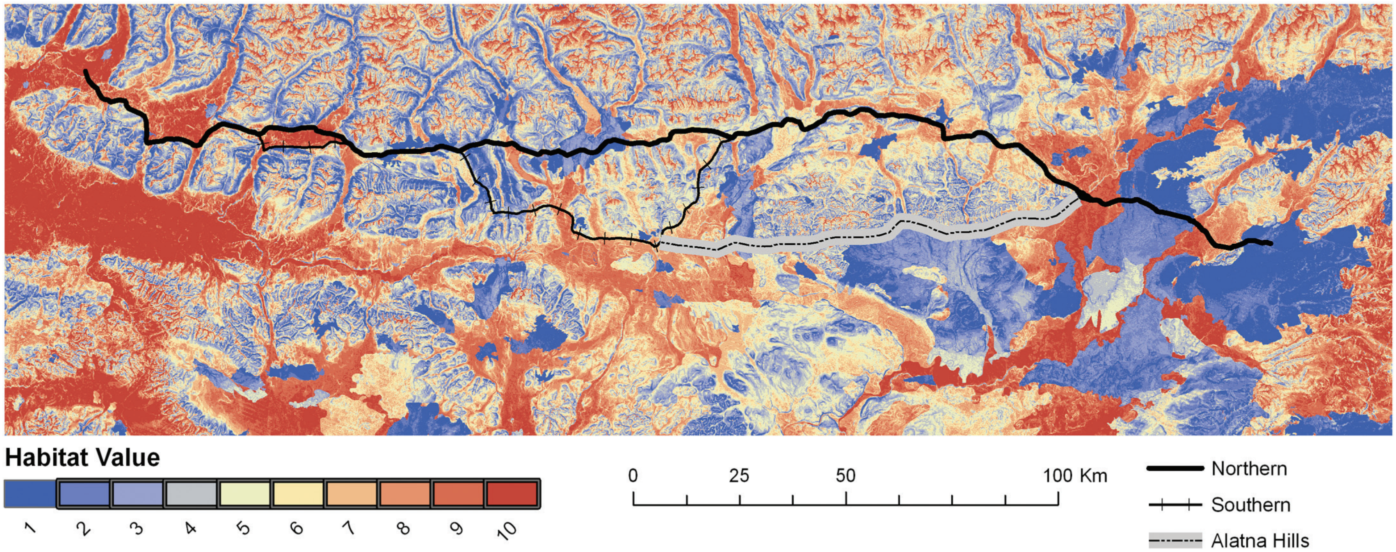

FIG. 3. Map of the three road study corridors connecting the Dalton Highway to the Ambler Mining District, Alaska, and predicted habitat values across the study area derived from the average of all competing step selection function models (ΔAIC ≤ 2). Predicted habitat values were classified into 10 quantiles ranging from low to high predicted habitat value. The top three bins were designated as high-value habitat for caribou in winter.

TABLE 3. Potential amount of high-value winter caribou habitat impacted by three road study corridors to the Ambler Mining District, Alaska, for three hypothetical scenarios of behavioral avoidance by caribou.

	High-value habitat lost					
	Northern route		Southern route		Alatna Hills route	
Disturbance Distance (km)	Area (km²)	Reduction (%)	Area (km²)	Reduction (%)	Area (km²)	Reduction (%)
1.0	151	1.5	171	1.7	146	1.5
2.5	387	3.9	436	4.4	380	3.8
5.0	740	7.4	848	8.5	752	7.6

level of reduction would be detrimental to the herd. Given that the study area represents only 13% of the herd's winter range (Joly et al., 2007) and was used, on average, by 10% of the population over the course of the study, it is unlikely that the level of habitat loss from the road alone would be sufficient to lead to population-level effects. Further, our results suggest that the high-value habitats that were diminished as a result of the road account for 1% or less of the total winter range of the herd. Caribou use of the study area was quite variable during our study, but the same area has been important winter range in the past (Skoog, 1968; Hemming, 1971). Thus, shifts in winter distribution could influence the importance of habitats in the vicinity of this road.

Our study also provided patterns of resource selection by caribou in the study area during winter. For example, our results indicated that caribou selected for older stands of lichen-bearing vegetation types. Additionally, we found that caribou selected for steep slopes (40%–60%) and more rugged terrain (relative to that available at different elevations across the study area) and for areas with less snow (as indexed by date of earliest snowmelt parameters). These results suggest that resource selection patterns during winter were primarily driven by caribou seeking areas where lichen availability and accessibility would be highest. Previous research on the winter range of the Western Arctic herd found that lichen abundance was four times lower in areas that had burned within 60 years (Joly et al., 2010) and that caribou tend to avoid those areas (Joly et al., 2003, 2007, 2010; Collins et al., 2011). Additionally, winds along exposed ridgelines and areas with shrubs help redistribute snow and create a variable matrix of snow conditions within an area (Liston et al., 2002; Bruland et al., 2004), helping to reduce the energetic costs of cratering to reach food (Fancy and White, 1985). Others have also observed a preference for cratering in areas with shallower, less dense snow cover (Collins and Smith, 1991; Johnson et al., 2001).

We estimated that the percentage of high-value habitat that would be reduced by the road is similar to the percentage that Polfus et al. (2011) estimated was lost to caribou in northern British Columbia adjacent to a small community. Thus, our estimates are within a reasonable range given the relatively low density of development expected from the road. However, other studies of the amount of winter habitat lost through avoidance by ungulates have shown significantly larger impacts. For example, mule deer (*Odocoileus hemionus*) in Wyoming could experience up to 60% habitat loss through avoidance of high-density natural gas drilling operations (Sawyer et al., 2009). Similarly, pronghorn (*Antilocapra americana*) were predicted to experience a five-fold reduction in high-value habitat as a result of natural gas facilities (Beckmann et al., 2012). Compared to these losses, the amount of habitat we expect to be lost as a result of avoidance behavior is considerably lower, but so is the expected level of development.

While the actual effect on caribou winter habitat will certainly differ from our predictions, estimating the potential effect on habitat of different development projects is important to help identify the least impactful development options to wildlife and allow managers to assess the trade-offs between different development options and their impacts to wildlife. Others have taken a similar approach to help inform development decisions as we did. For example, Wilson et al. (2013) showed that the development scenarios outlined for the National Petroleum Reserve-Alaska varied significantly in their potential to affect caribou calving habitat. Similarly, Brown et al. (2007) assessed the potential effects of various forest management strategies on woodland caribou habitat and found that the choice of strategy affected caribou habitat, but not the amount of timber that could be harvested. These types of methods have also been used for other taxa to predict the effects of different management decisions on populations. In the Intermountain West of the United States, Copeland et al. (2009) modeled the potential for sage grouse (*Centrocercus urophasianus*) leks to be lost as a result of different levels of predicted oil and gas development. Conversely, Bleich et al. (2010) modeled the predicted increase of bighorn sheep (*Ovis canadensis*) habitat in the Sierra Nevada Mountains of California with the development of additional man-made water sources. While none of these studies identified potential effects to winter caribou habitat, they all identified ways in which different management actions or land-use decisions could affect wildlife habitat.

While our estimates of habitat loss are small for this large herd, our assessment only considered one type of effect associated with the road: behavioral avoidance. Other factors must be considered for a full accounting of the potential effects of the road on caribou. For example, the energetic consequences of responding to traffic (at various levels) or displacing to areas with higher energetic costs (e.g., deeper snow; Fancy and White, 1987) could negatively affect caribou. Although occasional disturbance is not likely to be problematic (e.g., Tyler, 1991), increased energy costs accumulated over an entire winter could decrease productivity (White, 1983) and overwinter survival (Parker et al., 2009). Additional cumulative impacts that are important to consider are how sport hunting, subsistence, and recreational activities might change as a result of increased access to the area. In British Columbia, caribou were not observed in an area with intensive use by snowmobilers even though it was composed of high quality habitat (Seip et al., 2007). Even if the road is open only to traffic associated with industrial activities, there are no assurances that it will not lead to increased hunting or subsistence activities, especially in winter. Recently, Suárez et al. (2013) found that subsistence hunting along a road closed to non-industrial traffic increased at levels similar to levels of increase along a road with no such restrictions. Unrestricted access to the road could lead to greater levels of conflict between sport and subsistence hunters, further complicating management of the herd. Finally, just as the Dalton Highway has made the road to the Ambler Mining District possible, the road to Ambler will make further development possible beyond what we have considered. Indeed, roads have been proposed from Ambler to Nome, Kotzebue, and other locations in western Alaska that are currently roadless (DOWL HKM, 2011). Westward expansion of roads beyond Ambler has the potential to affect Western Arctic caribou and a greater portion of the herd's winter and other seasonal ranges (Joly, 2011).

Our prediction of minimal indirect losses to winter caribou habitat for the three proposed road routes to the Ambler Mining District relies on the assumption that range conditions will remain stationary through time. This likely will not be the case, especially given that lichens destroyed by fire will recover over time (Joly et al., 2010; Collins et al., 2011) and vegetation is projected to undergo changes associated with climate change (Euskirchen et al., 2009). Fire is anticipated to increase in the region (Joly et al., 2012), which could further reduce winter habitat quality in the study area, as we observed in its eastern portion. Indeed, the level of industrial development that caribou can tolerate before it affects the population has been shown to be a function of the percentage of habitat disturbed by fire in the past 50 years (Sorensen et al., 2008).

As the road planning process continues, it is still important to assess other factors that could alter the distribution of caribou or influence their population dynamics. Additional research is clearly needed to examine the effects on caribou that winter along the road corridor because space use and behavioral patterns can change quickly after development occurs (Sawyer et al., 2006; Harju et al., 2011). We believe the approach we took to address effects before development was initiated could serve as an example for resource managers. In particular, by using an objective set of methods to estimate the potential impacts to wildlife habitat from proposed development, resource managers could work with developers to find alternative locations or routes of infrastructure. Identifying these potential impacts early in the planning process allows for more time to make changes to the development plans—and ultimately, for more effective conservation of a population's habitat—than mitigation efforts after development occurs

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REFERENCES

Adamczewski, J.Z., Gates, C.C., Soutar, B.M., and Hudson, R.J. 1988. Limiting effects of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest Territories, Canada. Canadian Journal of Zoology 66(9):1986–1996.
http://dx.doi.org/10.1139/z88-291

Adams, L.G. 2003. Marrow fat deposition and skeletal growth in caribou calves. Journal of Wildlife Management 67(1):20–24.
http://dx.doi.org/10.2307/3803057

———. 2005. Effects of maternal characteristics and climatic variation on birth masses of Alaskan caribou. Journal of Mammalogy 86(3):506–513.
http://dx.doi.org/10.1644/1545-1542(2005)86[506:EOMCAC]2.0.CO;2

AICC (Alaska Interagency Coordination Center). 2013. Predictive services – maps/imagery/geospatial.
http://fire.ak.blm.gov/predsvcs/maps.php

Beckmann, J.P., Murray, K., Seidler, R.G., and Berger, J. 2012. Human-mediated shifts in animal habitat use: Sequential changes in pronghorn use of a natural gas field in Greater Yellowstone. Biological Conservation 147(1):222–233.
http://dx.doi.org/10.1016/j.biocon.2012.01.003

Bergerud, A.T., Luttich, S.N., and Camps, L. 2008. The return of caribou to Ungava. Montreal and Kingston: McGill-Queen's University Press.

Beyer, H.L., Haydon, D.T., Morales, J.M., Frair, J.L., Hebblewhite, M., Mitchell, M., and Matthiopoulos, J. 2010. The interpretation of habitat preference metrics under use-availability designs. Philosophical Transactions of the Royal Society B 365(1550):2245–2254.
http://dx.doi.org/10.1098/rstb.2010.0083

Bleich, V.C., Marshal, J.P., and Andrew, N.G. 2010. Habitat use by a desert ungulate: Predicting effects of water availability on mountain sheep. Journal of Arid Environments 74(6):638–645.
http://dx.doi.org/10.1016/j.jaridenv.2009.10.019

Boggs, K., Boucher, T.V., Kuo, T.T., Fehringer, D., and Guyer, S. 2012. Vegetation map and classification: Northern, western and interior Alaska. Anchorage: Alaska Natural Heritage Program, University of Alaska.

Boulanger, J., Poole, K.G., Gunn, A., and Wierzchowski, J. 2012. Estimating the zone of influence of industrial developments on wildlife: A migratory caribou *Rangifer tarandus groenlandicus* and diamond mine case study. Wildlife Biology 18(2):164–179.
http://dx.doi.org/10.2981/11-045

Brown, G.S., Rettie, W.J., Brooks, R.J., and Mallory, F.F. 2007. Predicting the impacts of forest management on woodland caribou habitat suitability in black spruce boreal forest. Forest Ecology and Management 245(1-3):137–147.
http://dx.doi.org/10.1016/j.foreco.2007.04.016

Bruland, O., Liston, G.E., Vonk, J., Sand, K., and Killingtveit, Å. 2004. Modelling the snow distribution at two High Arctic sites at Svalbard, Norway, and at an alpine site in central Norway. Nordic Hydrology 35(3):191–208.

Bunnefeld, N., Börger, L., van Moorter, B., Rolandsen, C.M., Dettki, H., Solberg, E.J., and Ericsson, G. 2011. A model-driven approach to quantify migration patterns: Individual, regional and yearly differences. Journal of Animal Ecology 80(2):466–476.
http://dx.doi.org/10.1111/j.1365-2656.2010.01776.x

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: A practical information–theoretic approach, 2nd ed. New York: Springer–Verlag.

Cameron, R.D., Smith, W.T., White, R.G., and Griffith, B. 2005. Central Arctic caribou and petroleum development: Distributional, nutritional, and reproductive implications. Arctic 58(1):1–9.
http://dx.doi.org/10.14430/arctic382

Collins, W.B., and Smith, T.S. 1991. Effects of wind-hardened snow on foraging by reindeer (*Rangifer tarandus*). Arctic 44(3):217–222.
http://dx.doi.org/10.14430/arctic1541

Collins, W.B., Dale, B.W., Adams, L.G., McElwain, D.E., and Joly, K. 2011. Fire, grazing history, lichen abundance, and winter distribution of caribou in Alaska's taiga. Journal of Wildlife Management 75(2):369–377.
http://dx.doi.org/10.1002/jwmg.39

Copeland, H.E., Doherty, K.E., Naugle, D.E., Pocewicz, A., and Kiesecker, J.M. 2009. Mapping oil and gas development potential in the US Intermountain West and estimating impacts to species. PLoS One 4(10): e7400.
http://dx.doi.org/10.1371/journal.pone.0007400

Cumming, H.G., and Hyer, B.T. 1998. Experimental log hauling through a traditional caribou wintering area. Rangifer Special Issue 10:241–258.
http://dx.doi.org/10.7557/2.18.5.1562

Dau, J. 2011. Units 21D, 22A, 22B, 22C, 22D, 22E, 23, 24, and 26A caribou management report. In: Harper, P., ed. Caribou management report of survey-inventory activities 1 July 2008–30 June 2010. Juneau: Alaska Department of Fish and Game. 187 – 250.

DOWL HKM. 2011. Ambler Mining District access preliminary hydrology reconnaissance memorandum. Anchorage: DOWL HKM.

Euskirchen, E.S., McGuire, A.D., Chapin, F.S., III, Yi, S., and Thompson, C.C. 2009. Changes in vegetation in northern Alaska under scenarios of climate change, 2003–2100: Implications for climate feedbacks. Ecological Applications 19(4):1022–1043.
http://dx.doi.org/10.1890/08-0806.1

Fancy, S.G., and White, R.G. 1985. Energy expenditures by caribou while cratering in snow. Journal of Wildlife Management 49(4):987–993.
http://dx.doi.org/10.2307/3801384

———. 1987. Energy expenditures for locomotion by barren-ground caribou. Canadian Journal of Zoology 65(1):122–128.
http://dx.doi.org/10.1139/z87-018

Festa-Bianchet, M., Ray, J.C., Boutin, S., Côté, S.D., and Gunn, A. 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: An uncertain future. Canadian Journal of Zoology 89(5):419–434.
http://dx.doi.org/10.1139/z11-025

Ficetola, G.F., and Denoël, M. 2009. Ecological thresholds: An assessment of methods to identify abrupt changes in species-habitat relationships. Ecography 32(6):1075–1084.
http://dx.doi.org/10.1111/j.1600-0587.2009.05571.x

Forester, J.D., Im, H.K., and Rathouz, P.J. 2009. Accounting for animal movement in estimation of resource selection functions: Sampling and data analysis. Ecology 90(12):3554–3565.
http://dx.doi.org/10.1890/08-0874.1

Fortin, D., Fortin, M.-E., Beyer, H.L., Duchesne, T., Courant, S., and Dancose, K. 2009. Group-size-mediated habitat selection and group fusion–fission dynamics of bison under predation risk. Ecology 90(9):2480–2490.
http://dx.doi.org/10.1890/08-0345.1

Gesch, D.B. 2007. The national elevation dataset. In: Maune, D., ed. Digital elevation model technologies and applications: The DEM user's manual. Bethesda, Maryland: American Society for Photogrammetry and Remote Sensing. 99–118.

Gustine, D.D., Parker, K.L., Lay, R.J., Gillingham, M.P., and Heard, D.C. 2006. Interpreting resource selection at different scales for woodland caribou in winter. Journal of Wildlife Management 70(6):1601–1614.
http://dx.doi.org/10.2193/0022-541X(2006)70[1601:IRSADS]2.0.CO;2

Gustine, D.D., Barboza, P.S., Lawler, J.P., Adams, L.G., Parker, K.L., Arthur, S.M., and Shults, B.S. 2012. Diversity of nitrogen isotopes and protein status in caribou: Implications for monitoring northern ungulates. Journal of Mammalogy 93(3):778–790.
http://dx.doi.org/10.1644/11-MAMM-A-164.1

Harju, S.M., Dzialak, M.R., Osborn, R.G., Hayden-Wing, L.D., and Winstead, J.B. 2011. Conservation planning using resource selection models: Altered selection in the presence of human activity changes spatial prediction of resource use. Animal Conservation 14(5):502–511.
http://dx.doi.org/10.1111/j.1469-1795.2011.00456.x

Hemming, J.E. 1971. The distribution and movement patterns of caribou in Alaska. Wildlife Technical Bulletin No. 1. Juneau: Alaska Department of Fish and Game. 60 p.

Johnson, C.J., Parker, K.L., and Heard, D.C. 2001. Foraging across a variable landscape: Behavioral decisions made by woodland caribou at multiple spatial scales. Oecologia 127(4):590–602.
http://dx.doi.org/10.1007/s004420000573

Johnson, C.J., Boyce, M.S., Case, R.L., Cluff, H.D., Gau, R.J., Gunn, A., and Mulders, R. 2005. Cumulative effects of human developments on Arctic wildlife. Wildlife Monographs 160. 36 p.

Joly, K. 2011. Modeling influences on winter distribution of caribou in northwestern Alaska through use of satellite telemetry. Rangifer Special Issue 19:75–85.
http://dx.doi.org/10.7557/2.31.2.1992

Joly, K., Dale, B.W., Collins, W.B., and Adams, L.G. 2003. Winter habitat use by female caribou in relation to wildland fires in interior Alaska. Canadian Journal of Zoology 81(7):1192–1201.
http://dx.doi.org/10.1139/z03-109

Joly, K., Bente, P., and Dau, J. 2007. Response of overwintering caribou to burned habitat in Northwest Alaska. Arctic 60(4):401–410.
http://dx.doi.org/10.14430/arctic197

Joly, K., Chapin, F.S., III, and Klein, D.R. 2010. Winter habitat selection by caribou in relation to lichen abundance, wildfires, grazing, and landscape characteristics in Northwest Alaska. Ecoscience 17(3):321–333.
http://dx.doi.org/10.2980/17-3-3337

Joly, K., Duffy, P.A., and Rupp, T.S. 2012. Simulating the effects of climate change on fire regimes in Arctic biomes: Implications for caribou and moose habitat. Ecosphere 3(5): art36.
http://dx.doi.org/10.1890/ES12-00012.1

Klein, D.R. 1982. Fire, lichens, and caribou. Journal of Range Management 35(3):390–395.
http://dx.doi.org/10.2307/3898326

Lele, S.R., Merrill, E.H., Keim, J., and Boyce, M.S. 2013. Selection, use, choice and occupancy: Clarifying concepts in resource selection studies. Journal of Animal Ecology 82(6):1183–1191.
http://dx.doi.org/10.1111/1365-2656.12141

Liston, G.E., McFadden, J.P., Sturm, M., and Pielke, R.A. 2002. Modelled changes in Arctic tundra snow, energy and moisture fluxes due to increased shrubs. Global Change Biology 8(1):17–32.
http://dx.doi.org/10.1046/j.1354-1013.2001.00416.x

Macander, M.J., and Swingley, C.S. 2012. Mapping snow persistence for the range of the Western Arctic caribou herd, Northwest Alaska, using the Landsat archive (1985–2011). Natural Resource Technical Report NPS/ARCN/NRTR—2012/643. Fort Collins, Colorado: National Park Service.

Murphy, S.M., and Curatolo, J.A. 1987. Activity budgets and movement rates of caribou encountering pipelines, roads, and traffic in northern Alaska. Canadian Journal of Zoology 65(10):2483–2490.
http://dx.doi.org/10.1139/z87-375

NCDC (National Climatic Data Center). 2013. Climate data online, Bettles, Alaska 1951–2012. Asheville, North Carolina: National Oceanic and Atmospheric Administration.
http://www.ncdc.noaa.gov

Nellemann, C., Vistnes, I., Jordhøy, P., and Strand, O. 2001. Winter distribution of wild reindeer in relation to power lines, roads and resorts. Biological Conservation 101(3):351–360.
http://dx.doi.org/10.1016/S0006-3207(01)00082-9

Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O., and Newton, A. 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. Biological Conservation 113(2):307–317.
http://dx.doi.org/10.1016/S0006-3207(03)00048-X

Northrup, J.M., and Wittemyer, G. 2013. Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. Ecology Letters 16(1):112–125.
http://dx.doi.org/10.1111/ele.12009

Parker, K.L., Barboza, P.S., and Gillingham, M.P. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology 23(1):57–69.
http://dx.doi.org/10.1111/j.1365-2435.2009.01528.x

Polfus, J.L., Hebblewhite, M., and Heinemeyer, K. 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. Biological Conservation 144(11):2637–2646.
http://dx.doi.org/10.1016/j.biocon.2011.07.023

R Development Core Team. 2012. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Russell, D.E., Martell, A.M., and Nixon, W.A.C. 1993. The range ecology of the Porcupine caribou herd in Canada. Rangifer Special Issue 8. 168 p.

Sappington, J.M., Longshore, K.M., and Thompson, D.B. 2007. Quantifying landscape ruggedness for animal habitat analysis: A case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71(5):1419–1426.
http://dx.doi.org/10.2193/2005-723

Sawyer, H., Nielson, R.M., Lindzey, F., and McDonald, L.L. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70(2):396–403.
http://dx.doi.org/10.2193/0022-541X(2006)70[396:WHSOMD]2.0.CO;2

Sawyer, H., Kauffman, M.J., and Nielson, R.M. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73(7):1052–1061.
http://dx.doi.org/10.2193/2008-478

Seip, D.R., Johnson, C.J., and Watts, G.S. 2007. Displacement of mountain caribou from winter habitat by snowmobiles. Journal of Wildlife Management 71(5):1539–1544.
http://dx.doi.org/10.2193/2006-387

Skoog, R.O. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. PhD thesis, University of California, Berkeley, California.

Sorensen, T., McLoughlin, P.D., Hervieux, D., Dzus, E., Nolan, J., Wynes, B., and Boutin, S. 2008. Determining sustainable levels of cumulative effects for boreal caribou. Journal of Wildlife Management 72(4):900–905.
http://dx.doi.org/10.2193/2007-079

Suárez, E., Zapata-Ríos, G., Utreras, V., Strindberg, S., and Vargas, J. 2013. Controlling access to oil roads protects forest cover, but not wildlife communities: A case study from the rainforest of Yasuní Biosphere Reserve (Ecuador). Animal Conservation 16(3):265–274.
http://dx.doi.org/10.1111/j.1469-1795.2012.00592.x

Therneau, T. 2013. A package for Survival Analysis in S. R package version 2.37-4.
http://cran.r-project.org/web/packages/survival/index.html

Tyler, N.J.C. 1991. Short-term behavioural responses of Svalbard reindeer *Rangifer tarandus platyrhynchus* to direct provocation by a snowmobile. Biological Conservation 56(2):179–194.
http://dx.doi.org/10.1016/0006-3207(91)90016-3

Vistnes, I., and Nellemann, C. 2008. The matter of spatial and temporal scales: A review of reindeer and caribou response to human activity. Polar Biology 31(4):399–407.
http://dx.doi.org/10.1007/s00300-007-0377-9

Weclaw, P., and Hudson, R.J. 2004. Simulation of conservation and management of woodland caribou. Ecological Modelling 177(1-2):75–94.
http://dx.doi.org/10.1016/j.ecolmodel.2003.12.052

White, R.G. 1983. Foraging patterns and their multiplier effects on productivity of northern ungulates. Oikos 40(3):377–384.
http://dx.doi.org/10.2307/3544310

Wilson, R.R., Prichard, A.K., Parrett, L.S., Person, B.T., Carroll, G.M., Smith, M.A., Rea, C.L., and Yokel, D.A. 2012. Summer resource selection and identification of important habitat prior to industrial development for the Teshekpuk caribou herd in northern Alaska. PLoS One 7(11): e48697.
http://dx.doi.org/10.1371/journal.pone.0048697

Wilson, R.R., Liebezeit, J.R., and Loya, W.M. 2013. Accounting for uncertainty in oil and gas development impacts to wildlife in Alaska. Conservation Letters 6(5):350–358.
http://dx.doi.org/10.1111/conl.12016

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. New York: Springer.
http://dx.doi.org/10.1007/978-0-387-87458-6