Mapping potential effects of proposed roads on migratory connectivity for a highly mobile herbivore using circuit theory

TImothy J. Fullman,1,7 Ryan R. Wilson,1,6 Kyle Joly,2 David D. Gustine,3 Paul Leonard,4 and Wendy M. Loya5

1The Wilderness Society, Anchorage, Alaska 99501 USA
2Gates of the Arctic National Park and Preserve, Arctic Inventory and Monitoring Network, National Park Service, Fairbanks, Alaska 99709 USA
3Grand Teton National Park, National Park Service, Moose, Wyoming 83012 USA
4Science Applications, U.S. Fish and Wildlife Service, Fairbanks, Alaska 99701 USA
5Science Applications, U.S. Fish and Wildlife Service, Anchorage, Alaska 99503 USA

Citation: Fullman, T. J., R. R. Wilson, K. Joly, D. D. Gustine, P. Leonard, and W. M. Loya. 2021. Mapping potential effects of proposed roads on migratory connectivity for a highly mobile herbivore using circuit theory. Ecological Applications 31(1):e02207. 10.1002/eap.2207

Abstract. Migration is common worldwide as species access spatiotemporally varying resources and avoid predators and parasites. However, long-distance migrations are increasingly imperiled due to development and habitat fragmentation. Improved understanding of migratory behavior has implications for conservation and management of migratory species, allowing identification and protection of seasonal ranges and migration corridors. We present a technique that applies circuit theory to predict future effects of development by analyzing season-specific resistance to movement from anthropogenic and natural environmental features across an entire migratory path. We demonstrate the utility of our approach by examining potential effects of a proposed road system on barren ground caribou (Rangifer tarandus granti) and subsistence hunters in northern Alaska. Resource selection functions revealed migratory selection by caribou. We tested five scenarios relating habitat selection to landscape resistance using Circuitscape and GPS telemetry data. To examine the effect of potential roads on connectivity of migrating animals and human hunters, we compared current flow values near communities in the presence of proposed roads. Caribou avoided dense vegetation, rugged terrain, major rivers, and existing roads in both spring and fall. A negative linear relationship between resource selection and landscape resistance was strongly supported for fall migration while spring migration featured a negative logarithmic relationship. Overall patterns of caribou connectivity remained similar in the presence of proposed roads, though reduced current flow was predicted for communities near the center of current migration areas. Such data can inform decisions to allow or disallow projects or to select among alternative development proposals and mitigation measures, though consideration of cumulative effects of development is needed. Our approach is flexible and can easily be adapted to other species, locations and development scenarios to expand understanding of movement behavior and to evaluate proposed developments. Such information is vital to inform policy decisions that balance new development, resource user needs, and preservation of ecosystem function.

Key words: Arctic; caribou; Circuitscape; development; disturbance; landscape resistance; management; migration; Rangifer tarandus.

INTRODUCTION

Migration is an important process for many species, with benefits including access to spatiotemporally varying resources and reduction of predators and parasites (Dingle and Drake 2007, Southwood and Avens 2010, Avgar et al. 2014, Brönmark et al. 2014). Migratory species contribute to ecological processes such as nutrient transport between diverse systems and temporary alteration of local trophic interactions (Brodersen et al. 2011, Bauer and Hoye 2014, Brönmark et al. 2014). These environmental effects also influence human food security, disease dynamics, and human–wildlife conflict and coexistence (Graham et al. 2009, Ziv et al. 2012, Liu et al. 2013, Hassell et al. 2017). Yet, migratory movements may be altered due to human development (Wilson et al. 2016) and long-distance migrations are becoming increasingly imperiled across the globe due to development and habitat fragmentation (Berger 2004,
Bolger et al. 2008, Wilcove and Wikelski 2008). Impediments to migration have often led to significant declines in populations (Bolger et al. 2008). Thus, improved understanding of migratory behavior not only can increase theoretical understanding of migration ecology, but also has implications for conservation and management of migratory species, allowing identification and possible protection of key seasonal ranges and migration corridors (Harris et al. 2009).

Land-use change and landscape fragmentation are increasing globally (Ibisch et al. 2016, Torres et al. 2016), and there is a need for adequate planning to minimize negative environmental effects of development activities. This is all the more important because adverse effects of development projects may persist for years, despite intensive mitigation efforts (Sawyer et al. 2017). Environmental assessments, such as those conducted under the National Environmental Policy Act (NEPA) in the United States, often rely on analyses of expected outcomes of proposed development activities on species, habitats, and people. In many cases, however, it can be challenging to predict the ecological effects of proposed development, highlighting the need for improved analyses to aid in environmental assessments. It is also increasingly recognized that natural and human systems cannot be managed separately, but rather are coupled together as wildlife and other natural systems increasingly interact with, affect, and are influenced by people (Liu et al. 2007, Carter et al. 2014).

We predict future effects of development by analyzing resource selection and resistance to movement across an entire migratory path from both anthropogenic and natural environmental features. We then use the resulting estimates of migratory resistance to project the expected impacts of potential development on migratory species and human resource users. While many connectivity studies for animal migration define resistance as the inverse of habitat suitability (Bond et al. 2017), this assumption has been questioned (Keeley et al. 2016, 2017, Ziolkowska et al. 2016). We directly test the assumption of inverse habitat suitability by exploring the relationship between habitat suitability and landscape resistance in a scenario testing framework. Scenario testing has long been a useful tool in conservation planning (Peterson et al. 2003), and we use it here by representing contrasting alternatives for responses of animals to their environment (sensu Cushman et al. 2006). Our scenarios evaluate alternative resistance landscapes using GPS-derived locations to select between alternatives.

We demonstrate the utility of our approach by applying it to one of the world’s longest terrestrial migrants: barren ground caribou (Rangifer tarandus granti) of the Western Arctic Herd (WAH) in northwestern Alaska (Joly et al. 2019). Caribou, along with related reindeer (R. t. tarandus), are the most abundant large terrestrial herbivore in the circumpolar arctic (Bråthen et al. 2007), spanning North America, Europe, and Asia (Festa-Bianchet et al. 2011, Mallory and Boyce 2018). Caribou are renowned for their long-distance migrations, covering hundreds to thousands of kilometers each year in some of the longest overland movements in the world (Fancy et al. 1989, Joly et al. 2019). During these movements, caribou influence vegetation and nutrient patterns through grazing and trampling (Stark et al. 2015, Heggenes et al. 2018) and serve as a prey species for brown bears (Ursus arctos), wolves (Canis lupus), and other predators (Reynolds and Garner 1987, Dale et al. 1994, Ballard et al. 1997, Mowat and Heard 2006, Magoun et al. 2018). Although widely distributed, many caribou and wild reindeer populations have faced large declines, likely due to global changes in climate and anthropogenic landscape change (Mallory and Boyce 2018).

Caribou play a central role in both food security and cultural well-being of many indigenous groups across the circumpolar arctic (Björklund 1990, Berkes et al. 1994, Braem 2012). Subsistence hunting, fishing, and gathering are important as sources of nutrition and to support culture, identity, and customary and traditional ways of life (Lambden et al. 2007, Smith et al. 2009, Fall 2018). In northwestern Alaska, subsistence harvest contributes substantially to food security, providing between 180–450 kg of wild foods per person per year (Magdanz et al. 2011). Caribou comprise a large part of this harvest. One survey of six villages found that between 37–118 edible kilograms of caribou were harvested per person per year (Braem 2012), with an individual caribou yielding about 53 kg of edible meat (Braem et al. 2011).

To inform management of caribou and their harvest, we apply circuit theory combined with empirical location data and landscape alternatives, using the results to represent migratory movement and habitat selection of caribou across broad spatial scales relevant to managing human impacts. Circuit theory can model movement of organisms across landscapes under an analogy of electrical current flowing across a resistance surface (McRae et al. 2008). Under circuit theory, cells in a landscape are treated as nodes in an electrical circuit that are connected to their neighboring cells with resistors that have strengths based on the landscape’s resistance to animal movement. Current is passed through the circuit from a source location, across the resistance landscape, and to a grounded destination. The resulting current value in each cell is proportional to the number of times a random walker travelling from the source to destination would be expected to pass through that cell (McRae et al. 2008). The approach has been applied to connectivity and gene flow for a wide range of taxa and environments (McRae and Beier 2007, Lawler et al. 2013, Braaker et al. 2014, Koen et al. 2014). While some have suggested that cost-distance approaches, such as least cost paths, may be more appropriate for modeling migratory connectivity (McClure et al. 2016), previous analysis of fall migratory movement for the WAH found that movement patterns better align with a random walk.
movement model, such as that underlying circuit theory
(Fullman et al. 2017).

Using our combination of circuit theory, GPS telemetry,
and landscape resistance scenarios, we analyze (1) which
landscape features are selected or avoided at the
scale of the entire migratory path of a caribou popula-
tion; (2) the season-specific relationship between relative
habitat suitability and environmental resistance during
caribou migration; (3) how migratory pathway suitabil-
ity is predicted to be affected by a proposed network of
roads; and (4) how road effects are expected to influence
subsistence hunters that rely on caribou.

**METHODS**

**Study area**

The WAH is the largest caribou herd in Alaska, with
~244,000 individuals as of July 2019 (A. Hansen,
personal communication). The herd occupies the northwest-
er portion of Alaska, covering a range of ~363,000 km²
(Fig. 1). Most caribou migrate north in the spring to
calve and spend the summer on the northern coastal
plain of Alaska and in the foothills and mountainous
regions of the Brooks Range (Dau 2011). In the fall,
most caribou migrate south to winter in the eastern Seward
Peninsula, Nulato Hills, and upper Kobuk River
(Joly et al. 2007, Dau 2013). The WAH is harvested for
subsistence by Alaska Native and other hunters from
over 40 communities in northwestern Alaska (Braem
2012), as well as by hunters from other parts of Alaska
and outside Alaska, who jointly comprise about 5% of
the annual harvest (Dau 2015).

**Caribou migration data**

We recorded caribou migration paths using GPS
telemetry data collected from 2009 to 2013. Adult female
caribou were fitted with GPS telemetry collars (Telonics
TGW-4680; Mesa, Arizona, USA) as they swam across
Onion Portage on the Kobuk River (Dau 1997, Joly
2011). Collars recorded location data every 8 h. The
Animal Care and Use Committee of the Alaska Depart-
ment of Fish and Game approved all animal handling
under protocol #2012-031R.

We determined start and end locations of migration
for each caribou using net-squared displacement (NSD;
Bunnefeld et al. 2011), with fall and spring migration

![Western Arctic Herd range.](image)

**FIG. 1.** Western Arctic Herd range. Caribou migrate each fall to their winter range, concentrating in the dark blue region in the
south. In the spring, they return to their calving range, indicated by the central dark blue region in the north. Existing gravel roads are
sparse within the region but the Arctic Strategic Transportation and Resources (ASTAR) project proposes a potential system of
roads across much of the herd’s northern range. Utilization intensity data provided by the Alaska Department of Fish and Game.
ASTAR roads digitized from an Alaska Department of Natural Resources map.
analyzed separately. In short, NSD describes the distance between a starting location and subsequent locations. For migratory species that feature clustered seasonal range use of repeated areas separated by persistent directed movement, NSD curves take on a characteristic shape in which values are initially low, increase rapidly during migration, level out, and then rapidly diminish. The start and end of the sharp increase and decrease in NSD values can be used to infer departure and arrival during migration (Bunnefeld et al. 2011). We used visual assessment of migration start and end from NSD plots (Mysterud et al. 2011) to avoid spurious results, as reported in previous studies (Mysterud et al. 2011, Bischof et al. 2012, Panzacchi et al. 2013).

**Identifying migratory habitat selection**

Resource selection occurs at a hierarchy of scales (Johnson 1980) and habitat selection patterns may differ across scales (Boyce et al. 2003). Because our interest was in selection at the scale of the entire migratory path, to understand areas used for migration out of the total annual range, we conducted a population-level resource selection function (RSF) analysis. We extracted fall and spring migration locations from the annual dataset using the migration start and end dates identified as described (see Caribou migration data). Generalized linear mixed effects (GLMM) models with random intercepts for year nested within each animal, run using the lme4 package (Bates et al. 2015) in R (version 3.6.1; R Core Team 2019), represented migration path selection by caribou separately for each season. We included 20 available points for each observed caribou location, based on a sample size sensitivity analysis (Northrup et al. 2013; Appendix S1). Available points were randomly generated across the study area, which we identified by a square bounding box slightly larger than the annual range of the herd (see Fig. 1 for annual herd range and Appendix S2: Fig. S1 for study area extent).

We investigated four environmental variables thought to influence caribou movement at broad scales: terrain ruggedness, major rivers, land cover, and existing roads (Appendix S2: Fig. S1). We calculated terrain ruggedness following Sappington et al. (2007), using three-dimensional vector dispersion to account for heterogeneity in both slope and aspect as a representation of topographic variability. The analysis used an eight-pixel moving window on a 60-m digital elevation model (Gesch 2007). We centered terrain ruggedness values by subtracting the mean and dividing by the standard deviation to aid model convergence. We obtained locations of first-order rivers, referred to here as “major rivers,” from the National Hydrography Dataset (NHD, available online) and converted their shapes to a raster using ArcGIS (ESRI, Redlands, California, USA). To represent broad land cover classes that might influence caribou migratory movements, we reclassified a 30-m composite map of Alaska land cover (Boggs et al. 2014) into three classes: open areas, dense vegetation, and burned areas (see Appendix S2: Table S1 for crosswalk). While large spans of open ocean are substantial barriers, caribou will cross sea ice (Miller et al. 2005, Joly 2012), thus near-shore coastal waters (within 3 km of the coast, plus all of Kotzebue Sound) that may at times be covered in sea ice were included as a fourth class: coastal waters (Appendix S2: Fig. S1). Open areas were used as the reference class in all RSF models.

Existing roads consisted of gravel and dirt roads including the Dalton Highway, roads associated with oil, gas and mining development, and roads extending from the town of Nome, Alaska (Fig. 1). We did not include small roads occurring within communities. To account for nonlinear responses of distance to road, we employed the approach of Carpenter et al. (2010, adapted from Nielsen et al. 2009). This featured an exponential distance decay function of the form $e^{-d/d_0}$, where $d$ was the distance from each used or available location to the nearest road in kilometers and $d_0$ was allowed to vary between seasons. This resulted in values ranging between 0 and 1 (Appendix S2: Fig. S1). With little clear theoretical basis on which to select the $d_0$ value, we tested a number of different $d_0$ values as well as a linear relationship with distance to roads using univariate GLMM models, selecting among them using Akaike’s Information Criterion corrected for small sample size ($AIC_c$; Burnham and Anderson 2002, Carpenter et al. 2010). We retained the best-performing metric to represent the influence of roads on caribou migration (Carpenter et al. 2010) and included this metric in our model selection described in the following paragraph. Candidate models included $d_0$ values every kilometer from 1–20, every 5 km from 25–50, every 10 km from 60–100, and every 50 km from 150–350 (Appendix S2: Tables S2, S3).

In an effort to align the functional grain (scale at which caribou may respond to landscape features or covariates) with the analysis grain (resistance surfaces) we chose to rescale environmental covariates to 1 km. This corresponds to the resolution at which road impacts on Alaskan caribou have previously been examined (Cameron et al. 1992, Joly et al. 2006, Johnson et al. 2020). This scale was also a compromise to achieve computational efficiency. Although we hypothesize that the functional grain may be larger than 1 km for some covariates, several studies have shown that when the analysis grain is finer than the functional grain, there is a small effect on the accuracy of resistance distance estimates (Cushman and Landguth 2010, Galpern and Manseau 2013). Investigation of variance inflation factors (VIFs) indicated collinearity was not an issue (all VIF values $<1.1$; Zuur et al. 2010, Dormann et al. 2013), so we created a set of candidate RSF models using a factorial combination of environmental variables, plus an intercept-only model, resulting in 16 total models. We
selected the top model for each season using AICc with the AICcmodavg R package (Mazerolle 2019). We evaluated predictive performance of the top models using k-fold cross-validation (Boyce et al. 2002, Johnson et al. 2006) by splitting the caribou location data for each seasonal migration into 10 parts, with 90% of the data used to train the model and 10% of the data withheld to test the model in each fold. We visualized the relative probability of selection by caribou with respect to distance from roads using model-based parametric bootstrapping with the bootMer function in lme4 (Bates et al. 2015). For each season, 500 bootstrap simulations provided estimates of the mean response and 95% confidence interval of caribou relative selection with respect to roads. We held all other variables at their mean (terrain ruggedness) or baseline (river = 0, land cover = open areas) levels when creating these predictions.

Resistance scenario testing

While resistance to animal movement is often assumed to be the inverse of habitat suitability, animals may display more complicated resistance relationships with their environment (Braaker et al. 2014, Keeley et al. 2017). We examined the relationship between relative habitat suitability and landscape resistance directly by analyzing five resistance scenarios (Table 1, Appendix S2: Figs. S2 and S3; Braaker et al. 2014). These ranged from having resistance related only to distance (r0), to a positive relationship with habitat suitability (r1), to three variants of negative relationships between resistance and suitability, varying in the degree to which high resistance or low resistance predominates across the landscape (r2–r4; Table 1). Resistance values under each model, except the neutral (r0), were stretched to range between 1–1,000. It is the relative magnitude of resistance variables, rather than their specific values, that is informative when evaluating between alternatives (Cushman et al. 2006).

We used circuit theory to investigate which resistance scenario best fit the data for WAH fall and spring migration routes. We modeled expected flow of caribou under the various resistance landscapes using Circuitscape (version 4.0.5; Shah and McRae 2008) in raster mode with pairwise calculation and connectivity calculated using a cell’s eight nearest neighbors. The start and end points in each caribou’s migration path (see Caribou migration data) defined source and ground locations, respectively, for electrical current density (i.e., “flow”) in the Circuitscape model. We generated cumulative maps of current flow for each caribou–season–year–scenario combination. See Data S1 for an example initiation file for Circuitscape.

Caribou GPS data allowed us to determine support among alternative resistance scenarios. We extracted current flow values produced by Circuitscape for each resistance scenario at all recorded locations along the migration path for an individual using the raster package (Hijmans 2019) in R. Summing these values yielded the total current flow for a given resistance scenario. We ranked the underlying resistance scenarios for each individual, with the highest summed current flow at observed caribou locations yielding the best ranking. We tabulated the number of times each resistance scenario appeared as a top-ranked model to demonstrate the consistency of support for each resistance relationship across individuals, inferring greater confidence in resistance scenarios that consistently appeared in the top-ranked models compared to a scenario more evenly spread among rankings. We mapped population-level connectivity for fall and spring migration across the WAH range by summing the top-ranked maps for each individual after standardizing each raster to sum to one. K-fold cross-validation with 10 folds indicated model performance for the population-level connectivity layers. Example code for all analyses can be found in Data S1.

Evaluating effects of a proposed road system

We used the observed responses of caribou to existing roads (see Results) to predict the potential effects of a proposed system of roads on the flow of caribou during migration. In 2017, the Alaska Department of Natural Resources initiated the Arctic Strategic Transportation and Resources (ASTAR) project. The project encompassed a three-year effort to develop a strategic plan to re-write existing management policy and support creation of roads and other infrastructure between communities and resource development areas (Mack 2017). Publicly posted maps depicted potential routes for ASTAR roads that cross the WAH range (Fig. 1). We downloaded and digitized the ASTAR proposal map (DNR 2017). This map was not intended to represent final locations of ASTAR roads, but rather represents one realistic depiction of the location of future roads in an area that currently is predominantly roadless. As such, it presented an opportunity to demonstrate the ability of our approach to examine effects of potential roads on caribou migration.

We generated a resistance landscape for each caribou using the top-ranked scenario identified for that individual. In this resistance landscape, the season-specific road

| Resistance scenario | Relationship | Formula |
|---------------------|--------------|---------|
| r0: Neutral         | all equal    | r = 1   |
| r1: Positive linear | positive     | r = hs  |
| r2: Negative exponential | mostly low resistance | r = (1/hs)² |
| r3: Negative linear | negative     | r = (1/hs) |
| r4: Negative logarithmic | mostly high resistance | r = ln(1/hs) |

Notes: r, landscape resistance to movement; hs, relative habitat suitability. See Appendix S2: Figs. S2 and S3 for maps of resistance landscapes under each scenario for fall and spring migration, respectively.
selection distance decay functions and coefficients identified in the above analysis were applied to both existing roads and possible future roads (Appendix S2: Figs. S4 and S5). Similar to the creation of the population-level connectivity maps described above, we ran Circuitscape on each of these resistance landscapes and summed the standardized results to represent population-level connectivity in the presence of the proposed road system.

To examine the effects of potential roads on connectivity of migrating caribou and subsistence hunters, we compared current flow values near communities in the presence and absence of proposed roads. Point locations of communities within the range of the herd (Appendix S2: Fig. S6), buffered by 20 km, represented easily accessible caribou hunting areas. While subsistence hunting of caribou occurs across wide areas (Brinkman et al. 2014), analysis from western Canada reported preferences for and highest use of hunting near communities in areas accessible during day trips (Berman and Kofinas 2004). Variability exists, however, in area covered for subsistence harvest among different communities in northwestern Alaska and within communities, such as based on hunter age and gender (Satterthwaite-Phillips et al. 2016). We extracted current flow values within the 20 km buffers from the population-level current flow maps with and without possible roads included and calculated effect sizes for each community using raw score standardization, since our interest was in differences with and without possible roads (Morris and DeShon 2002). We used the thresholds suggested by Cohen (1992) to represent the approximate levels of effect.

**RESULTS**

Location data represented 57 caribou for fall migration and 70 caribou for spring migration. Collars provided one to four years of location information per caribou, resulting in 131 fall migrations and 153 spring migrations (referred to here as “individuals”). We did not conduct a study of collar location accuracy as part of this project, however, previous work with similar collars reported an average location error of 33 m (Joly 2005), well within the resolution of our covariate data.

Model selection analysis of the effect of roads on caribou locations indicated strong support for exponential decay over a linear relationship with distance (Appendix S2: Tables S2 and S3). For fall migration, a decay function of 60 km was most strongly supported, with $\Delta$AIC$_c > 2$ compared to the next closest model and 87% of the Akaike weight (Appendix S2: Table S2). Results in spring were more evenly mixed, with alpha values of 12, 13, 14, and 15 km all within 2 AIC$_c$ of the best-supported model (Appendix S2: Table S3). We followed Carpenter et al. (2010) and retained only the best-performing metric ($\alpha = 14$) as a representation of the effect of roads on caribou migration in subsequent models for spring migration.

Comparison of caribou resource selection models using AIC$_c$ indicated strong support for the full model, containing all four environmental variables, in both fall and spring (Appendix S2: Tables S4 and S5). Resource selection patterns were similar in both seasons (Table 2). Caribou showed negative responses to increasing terrain ruggedness and the presence of major rivers, and showed greater avoidance of dense vegetation, burned areas, and coastal areas relative to open land cover types. Prediction of relative probability of selection at increasing distances from roads, with all other coefficients held at their mean or baseline values, indicated a low probability of selection near roads (Fig. 2). Road avoidance was stronger in spring compared to fall (Table 2, Fig. 2). All coefficients had 95% confidence intervals that did not overlap zero. $K$-fold cross-validation indicated high predictive performance of resource selection models in both seasons, as denoted by Spearman-rank correlation ($\rho_{\text{fall}} = 0.96, \rho_{\text{spring}} = 0.95$).

Considering resistance scenario rankings among individuals, support for different scenarios varied between individuals, but scenario r3 was the most common top-ranked model for fall migration, occurring in about 75% of the top-ranked models (Fig. 3a, Appendix S2: Table S6). In the spring, r3 featured in nearly 30% of the top-ranked models, but was surpassed by r4, which was featured in 66% of the top-ranked models (Fig. 3b, Appendix S2: Table S7). Scenario r2 was not ranked as a top model by any individual in the spring.

Population-level connectivity maps for fall (Fig. 4a) and spring (Fig. 4b) migration revealed differences in the concentration of current flow between seasons. Both seasons showed similar areas of high connectivity in the south of the study area, though with greater intensity in spring than fall. Connectivity in the north differed across seasons, however, with spring featuring a strong concentration of high current flow and fall exhibiting more diffuse connectivity. $K$-fold cross-validation, reflecting how well population-level current flow maps represent observed caribou locations, demonstrated high

| Environmental variable | Fall Estimate (SE) | Spring Estimate (SE) |
|------------------------|-------------------|----------------------|
| Intercept              | -4.17 (0.03)      | -14.04 (0.21)        |
| Ruggedness             | -0.22 (0.01)      | -0.20 (0.01)         |
| Major rivers           | -0.56 (0.04)      | -0.28 (0.04)         |
| Distance decay from roads† | 2.45 (0.04)     | 12.74 (0.23)         |
| Dense vegetation‡      | -1.17 (0.02)      | -1.56 (0.03)         |
| Burned areas‡          | -0.26 (0.07)      | -1.33 (0.14)         |
| Coastal areas‡         | -2.82 (0.13)      | -2.69 (0.14)         |

†Distance decay followed $e^{-\alpha d}$ where $d$ is distance in km and $\alpha = 60$ in fall, 14 in spring.
‡Selection reported relative to the open areas reference class.

Table 2. Top model results for caribou resource selection during fall and spring migration.
predictive ability of the models in both seasons ($\hat{\rho}_{\text{fall}} = 0.95$, $\hat{\rho}_{\text{spring}} = 0.94$). Average connectivity values at observed caribou locations were higher than across the study area in both fall (mean $\pm$ SE at caribou locations: $6.6 \times 10^{-4} \pm 1.9 \times 10^{-5}$, study area mean: $2.4 \times 10^{-5}$) and spring (caribou locations: $9.1 \times 10^{-4} \pm 1.4 \times 10^{-5}$, study area: $2.8 \times 10^{-4}$).

Adding a possible road system to the resistance landscape altered current flow patterns in both fall and spring, although overall patterns remained similar (Fig. 4c, d). Analysis of effect sizes indicated varying results for alteration of current flow near communities both over space and across seasons (Fig. 5). Communities in the southwest of the study area generally showed negligible change in current flow during fall migration with the addition of proposed roads, while those along the eastern periphery showed increased flow (Appendix S2: Fig. S7). Communities just to the east of the primary migration areas, as well as those to the north, showed decreases in current flow in fall. In spring, more communities showed increases in current flow compared to fall, though there were exceptions (e.g., Kotzebue, Shugnak) where current flow switched from expected increase to decrease across seasons.

**DISCUSSION**

Our analytical approach revealed broad-scale landscape features that influenced the use of migration paths by caribou in northwestern Alaska. It further demonstrated potential impacts of a proposed road system on movement of a highly mobile species and the people who rely on it for hunting. Such understanding is vital to inform permitting decisions that balance new development, resource user needs, and the preservation of ecosystem function. Our methods are flexible and can easily be adapted to other species, locations, and development scenarios.

Caribou patterns of resource selection during migration generally aligned with relationships previously reported for the WAH. For example, the negative responses to rugged terrain, major rivers, and dense vegetation recorded in this study also were identified for WAH fall migration by Fullman et al. (2017). Dense vegetation, typically tall shrubs, may increase predation risk for caribou (Bergerud and Luttich 2003, Joly and Klein 2011, Pinard et al. 2012) and form a physical barrier to
movement. The migratory period is a time of heightened wolf predation for the WAH (Ballard et al. 1997, Gurarie et al. 2020), favoring actions that reduce this risk. Avoidance of burned areas aligns with previous studies of caribou winter habitat use, where it has been related to reduced forage availability (Joly et al. 2003, 2007, Collins et al. 2011). The negative response of caribou to rugged terrain likely reflects increased energetic costs for migratory movements due to greater movement tortuosity (Wilson et al. 2013a) and the increased effort required to climb slopes (Fancy and White 1987), though studies have shown that caribou select more varied topography at fine scales (Joly 2011, Wilson et al. 2014) due to increased forage availability (Nellemann and Thomsen 1994, Nellemann and Fry 1995).

Selection of areas farther from existing roads was clearly indicated across both seasons, despite the paucity of roads in the study area. Multiple studies have found that caribou and reindeer may show avoidance or altered movement behavior in proximity to roads (Leblond et al. 2003, 2007, Collins et al. 2011).

**FIG. 4.** Population-level migratory connectivity for the Western Arctic Herd in (a) fall with existing roads, (b) spring with existing roads, (c) fall with possible roads added, and (d) spring with possible roads added. Maps display summed current flow values under each individual’s top-ranked model for the given season. Start and end locations are the same within seasons.
2013, Panzacchi et al. 2013, Wilson et al. 2016, Baltensperger and Joly 2019) and that road effects may extend beyond their physical footprint due to noise, dust, human activity, and other factors (Myers-Smith et al. 2006, Shannon et al. 2014, Paton et al. 2017). While our study finds a negative response to roads during migration, this does not imply that roads pose an absolute barrier. Future studies should quantify both the degree of permeability of roads for caribou (Beyer et al. 2016) and drivers of permeability (e.g., landscape context, road type, traffic), as these factors likely have a strong influence on the overall impact of roads on caribou (Muhly et al. 2015). Other potential concerns also need to be investigated, such as the possibility of roads increasing vulnerability to predators (Whittington et al. 2011, Bojarska et al. 2017, Newton et al. 2017). Additionally, there may be road density threshold effects where the cumulative impacts of additional roads could result in the failure of migration altogether.

Results for caribou subsistence hunters under a realistic road system proposal were mixed. While the overall pattern of caribou connectivity remained similar (Fig. 4), our models predicted altered current flow with the addition of proposed roads that led to reductions in caribou flow for several communities near the center of current migration areas (Appendix S2: Fig. S7). These predictions should receive careful consideration as new projects are being planned to ensure that resource
development opportunities do not end up undermining subsistence opportunities, as has been suggested in other countries (Parlee et al. 2018). Some communities may be able to substitute reductions in caribou availability with other resources (e.g., marine mammals), while for others that are highly dependent on caribou the impacts may be felt more strongly (Anaktuvuk Pass; Bacon et al. 2011, Martin 2015). It is possible that changes in caribou movement patterns in response to new development may increase subsistence opportunities for some communities, as is suggested for communities in the southern and eastern portions of the study area. However, the effects of new roads are likely to be complicated. They may increase access for subsistence hunting, potentially compensating for altered caribou flow near communities. At the same time, they may facilitate access by non-local hunters, which could reduce subsistence harvest success (Guettabi et al. 2016). In northwest Alaska, there are already reports of user conflict between hunters from within and outside of the region (Georgette and Loon 1988, Fix and Harrington 2012, Halas 2015). Hunting around potential roads may compound road effects on species movement, leading to increased avoidance of roads by caribou (Paton et al. 2017, Plante et al. 2018). Furthermore, other future development such as the Ambler Road, which is currently undergoing permitting for access to the Ambler Mining District and is proposed to run through the southeastern part of the study area (BLM 2019), could result in cumulative effects when combined with the possible roads evaluated in our analysis, altering the consequences for communities in the region. The potential for cumulative effects, altered access and increased user conflict should be considered in future analyses of any road proposals.

Our findings are not the final word on impacts from a possible road system in the area. Planning for the ASTAR project is ongoing and community consultations have yet to be held in many places. The routes and lengths of proposed roads have already been modified multiple times and we expect there will be further modifications prior to any roads being built. Furthermore, analysis of potential road impacts on caribou is just one of many analyses that would need to be conducted prior to a road project being developed. Mitigation measures (e.g., reduced speed limits, closures during migration, and over- or underpasses) may further alter resistances experienced by caribou relative to our analysis, although impacts to migratory movements were still noted in the presence of mitigation measures along the road to the Red Dog Mine within our study area (Wilson et al. 2016). Finally, full evaluation of potential impacts of road system proposals should consider effects on wildlife species during their complete annual cycle. For example, in the road system proposal we evaluated, the WAH calving area is bisected by three roads. Sensitivity of calving caribou and those with young calves has been noted around oil and gas development in other parts of northern Alaska (Griffith et al. 2002, Cameron et al. 2005, Joly et al. 2006). Methods for analyzing potential development impacts on habitat selection of caribou in other seasons already exist (Wilson et al. 2013b, 2014) and should be complemented by our migration-focused approach, or other similar methods, to provide a more robust representation of the cumulative effects of potential road systems.

Utility of our approach

We applied circuit theory to examine broad-scale selection in the context of entire migration pathways and to examine the relationship between landscape resistance and relative habitat suitability. For fall migration, a negative linear relationship between habitat suitability and landscape resistance was strongly supported for most caribou (Fig. 3a, Appendix S2: Table S6), aligning with one of the most commonly used approaches to deriving resistance surfaces from resource selection studies (Zeller et al. 2012). The different pattern observed for spring migration, with about two-thirds of caribou migrations indicating the negative logarithmic as their top-ranked resistance model (Fig. 3b, Appendix S2: Table S7), reinforces the importance of incorporating season-specific resistance rasters (Cushman and Lewis 2010, Mui et al. 2017). The strength of resistance relationships can change across seasons, even if the patterns of RSF coefficients remain similar.

While this study focused on caribou, our approach can readily be applied to other migratory species. In addition, our approach is applicable beyond migration and can be used to understand selection during other types of directed movement in which start and end locations are known and spatial data are available along the movement route. As such, circuit theory provides the opportunity to expand our understanding of multiple movement behaviors and to test hypotheses about how landscape resistance relates to habitat selection.

Myriad studies exist analyzing effects of existing roads and other development on wildlife connectivity (Lendrum et al. 2012, Ito et al. 2013, Prokopenko et al. 2017, Plante et al. 2018, Quaglietta et al. 2019), but fewer consider the effects of future or proposed roads. Most studies that do consider proposed roads utilize simulation models (Finke et al. 2008, Holdo et al. 2011, Davey et al. 2017). We provide an empirically based analytical approach to assessing proposed road impacts using animal movement data. Genetic analyses provide an alternative approach to assess landscape resistance and development impacts (Epps et al. 2007). In situations where this type of information is not available, our approach provides a means to identify movement resistance and development impacts.

Conservation and policy implications

Disruption of migration routes has at times led to sudden and severe population declines for migratory species
(Bolger et al. 2008). The consequences of disrupted migrations may ripple out to negatively affect other ecosystem components, such as predators that rely on migratory species (Walton et al. 2017) or alternative prey species that face increased pressure from predators when migrants are removed (Lee et al. 2016). In places like the Arctic, disrupted migration could also affect subsistence harvests. It is thus crucial to conduct development projects in a way that minimizes hindrances to migration. When making decisions, it is necessary to decide when adverse impacts are considered acceptable and when they should lead to restrictions on, or mitigation of, activities (Gende et al. 2018). Examining potential effects of roads and other developments before they are constructed is an important step in this direction, facilitating informed discussions with stakeholders and communities about the advantages and disadvantages of alternative proposals. Our approach, using circuit theory to evaluate potential impacts of proposed development while simultaneously selecting between alternative landscape resistance scenarios, presents one technique to better inform such discussions and planning.

ACKNOWLEDGMENTS

Comments from Jim Dau, John Pearce, and anonymous reviewers improved earlier versions of this manuscript. Caribou captures were a collaborative effort involving the Alaska Department of Fish and Game, Bureau of Land Management, National Park Service, U.S. Fish and Wildlife Service, and regional high schools. Support for TJF was provided by grants from the Wilburforce Foundation. Use of any trade names in this manuscript does not imply endorsement by the U.S. Government.

LITERATURE CITED

Avgar, T., G. Street, and J. M. Fryxell. 2014. On the adaptive benefits of mammal migration. Canadian Journal of Zoology 92:481–490.

Bacon, J. J., T. R. Hepa, H. K. Jr Brower, M. Pedersen, T. P. Olemaun, J. C. George, and B. G. Corrigan 2011. Estimates of subsistence harvest for villages on the North Slope of Alaska, 1994–2003. Department of Wildlife Management, North Slope Borough, Barrow, Alaska, USA.

Ballard, W. B., L. A. Ayres, P. R. Krausman, D. J. Reed, and S. G. Fancy. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs 135:3–47.

Balentsperger, A. P., and K. Joly. 2019. Using seasonal landscape models to predict space use and migratory patterns of an arctic ungulate. Movement Ecology 7:18.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bauer, S., and B. J. Hoye. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. Science 344:124252.

Berger, J. 2004. The last mile: how to sustain long-distance migration in mammals. Conservation Biology 18:320–331.

Bergerud, A. T., and S. N. Luttich. 2003. Predation risk and optimal foraging trade-off in the demography and spacing of the George River Herd, 1958 to 1993. Rangifer 14:169–191.

Berkes, F., P. J. George, R. J. Preston, A. Hughes, J. Turner, and B. D. Cummins. 1994. Wildlife harvesting and sustainable regional native economy in the Hudson and James Bay Lowland, Ontario. Arctic 47:350–360.

Berman, M., and G. Kofinas. 2004. Hunting for models: Grounded and rational choice approaches to analyzing climate effects on subsistence hunting in an Arctic community. Ecological Economics 49:31–46.

Beyer, H. L., E. Gurarie, L. Börger, M. Panzacchi, M. Basille, I. Herfindal, B. Van Moorter, S. R. Lele, and J. Matthiopoulos. 2016. “You shall not pass!”: quantifying barrier permeability and proximity avoidance by animals. Journal of Animal Ecology 85:43–53.

Bischof, R., L. E. Loe, E. L. Meisingset, B. Zimmermann, B. van Moorter, and A. Mysterud. 2012. A migratory northern ungulate in the pursuit of spring: jumping or surfing the green wave? American Naturalist 180:407–424.

Bjorklund, I. 1990. Sámi reindeer pastoralism as an indigenous resource management system in Northern Norway: A contribution to the common property debate. Development and Change 21:75–86.

BLM (Bureau of Land Management). 2019. Ambler Road Draft Environmental Impact Statement. Bureau of Land Management, U.S. Department of the Interior, Fairbanks, Alaska, USA.

Boggs, K., T. V. Boucher, T. T. Kuo, D. Fehringer, and S. Gayer. 2014. Vegetation map and classification: northern, western and interior Alaska. Alaska Center for Conservation Science (formerly Alaska Natural Heritage Program), University of Alaska Anchorage, Anchorage, Alaska, USA. http://accs.uaa.alaska.edu/vegetation-ecology/vegetation-map-northern-western-and-interior-alaska/

Bojaraska, K., M. Kwiatkowska, P. Skórka, R. Gula, J. Theuerkauf, and H. Okarma. 2017. Anthropogenic environmental traps: Where do wolves kill their prey in a commercial forest? Forest Ecology and Management 397:117–125.

Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11:63–77.

Bond, M. L., C. M. Bradley, C. Kiffner, T. A. Morrison, and D. E. Lee. 2017. A multi-method approach to delineate and validate migratory corridors. Landscape Ecology 32:1705–1721.

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, K. A., R. A. Ims, N. G. Yoccoz, P. Fauchald, T. A. Morrison, and D. J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecology 10:421–431.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Braaker, S., M. Moretti, R. Boesch, J. Ghazoul, M. K. Obrist, and F. Bontadina. 2014. Assessing habitat connectivity for ground-dwelling animals in an urban environment. Ecological Applications 24:1583–1595.

Braem, N. M. 2012. subsistence wildlife harvests in Ambler, Buckland, Kiana, Kobuk Shaktoolik and Shishmaref, Alaska, 2009–2010. Special Publication No. SP2012-003. Alaska Department of Fish and Game Division of Subsistence, Fairbanks, Alaska, USA.

Braem, N. M., S. Pedersen, J. Simon, D. Koster, T. Kaleak, P. Leavitt, J. Palkotak, and P. Neakok. 2011. Monitoring of annual caribou harvests in the National Petroleum Reserve Alaska: Atqasuk, Barrow, and Nuiqsut, 2003–2007. Technical Paper No. 361. Alaska Department of Fish and Game, Division of Subsistence, Fairbanks, Alaska, USA.

Brathen, K. A., R. A. Ims, N. G. Yoccoz, P. Fauchald, T. TVeraa, and V. H. Hausner. 2007. Induced shift in ecosystem
productivity? Extensive scale effects of abundant large herbivores. Ecosystems 10:773–789.

Brinkman, T., K. B. Maracle, J. Kelly, M. Vandyke, A. Firmin, and A. Springsteen. 2014. Impact of fuel costs on high-latitude subsistence activities. Ecology and Society 19:18.

Brodersen, J., A. Nicolle, P. A. Nilsson, C. Skov, C. Brönmark, and L.-A. Hansson. 2011. Interplay between temperature, fish partial migration and trophic dynamics. Oikos 120:1838–1846.

Brönmark, C., K. Hultén, P. A. Nilsson, C. Skov, L.-A. Hansson, J. Brodersen, and B. B. Chapman. 2014. There and back again: migration in freshwater fishes. Canadian Journal of Zoology 92:467–479.

Bunnefeld, N., L. Börger, B. van Moorter, C. M. Rolandes, H. Dettke, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466–476.

Burnham, K. P., and D. R. Anderson 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Cameron, R. D., D. J. Reed, J. R. Dau, and W. T. Smith. 1992. Redistribution of calving caribou in response to oil field development on the Arctic Slope of Alaska. Arctic 45:338–342.

Cameron, R. D., W. T. Smith, R. G. White, and B. Griffith. 2005. Central arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. Arctic 58:1–9.

Carpenter, J., C. Aldridge, and M. S. Boyce. 2010. Sage-grouse habitat selection during winter in Alberta. Journal of Wildlife Management 74:1806–1814.

Carter, N. H., A. Viña, V. Hull, W. J. McConnell, W. Axinn, D. Ghmire, and J. Liu. 2014. Coupled human and natural systems approach to wildlife research and conservation. Ecology and Society 19:43.

Cohen, J. 1992. A power primer. Psychological Bulletin 112:155–159.

Collins, W. B., W. D. Dale, L. G. Adams, D. E. McElwain, and K. Joly. 2011. Fire, grazing history, lichen abundance, and winter distribution of caribou in Alaska’s taiga. Journal of Wildlife Management 75:369–377.

Cushman, S. A., and E. L. Landguth. 2010. Scale dependent inference in landscape genetics. Landscape Ecology 25:967–979.

Cushman, S. A., and J. S. Lewis. 2010. Movement behavior explains genetic differentiation in American black bears. Landscape Ecology 25:1613–1625.

Cushman, S. A., K. S. McKevel, J. Hayden, and M. K. Schwartz. 2006. Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. American Naturalist 168:486–499.

Dale, B. W., L. G. Adams, and R. T. Bowyer. 1994. Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. Journal of Animal Ecology 63:644–652.

Dau, J. 1997. Units 21D, 22A, 22B, 22C, 22D, 22E, 23, 24, and 26A caribou management report. Pages 158–185 in M. Hicks, editor. Caribou management report of survey and inventory activities 1 July 1994 – 30 June 1996. Alaska Department of Fish and Game, Juneau, Alaska, USA.

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

Dau, J. R. 2015. Units 21D, 22A, 22B, 22C, 22D, 22E, 23, 24 and 26A. Pages 14–1 to 14–89 in P. Harper, and McCarthy, L. A., editors. Caribou management report of survey and inventory activities 1 July 2012–30 June 2014. Species Management Report ADF&G/DWC/SMR-2013-5. Alaska Department of Fish and Game, Juneau, Alaska, USA.

Davae, N., S. Dunstall, and S. Halgambu. 2017. Optimal road design through ecologically sensitive areas considering animal migration dynamics. Transportation Research Part C 77:478–494.

Dingle, H., and V. A. Drake. 2007. What is migration? BioScience 57:113–121.

DNR (Alaska Department of Natural Resources). 2017. Arctic Strategic Transportation and Resources—ASTAR. Originally obtained from http://soa-dnr.maps.arcgis.com/apps/MapSeries/index.html?appid=632aa463ac314be9e963e60bb40a396d. Now available at http://soa-dnr.maps.arcgis.com/apps/Cas/index.html?appid=ab8be9349a847ebfe6d6d17e00c8d6. Dornm, C. F. et al 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashears. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44:714–724.

Fall, J. A. 2018. Subsistence in Alaska: A year 2017 update. Division of Subsistence, Alaska Department of Fish and Game, Anchorage, Alaska, USA.

Fancy, S. G., L. F. Pank, K. R. Whitten, and W. L. Regelin. 1989. Seasonal movements of caribou in arctic Alaska as determined by satellite. Canadian Journal of Zoology 67:644–650.

Fancy, S. G., and R. G. White. 1987. Energy expenditures for locomotion by barren-ground caribou. Canadian Journal of Zoology 65:122–128.

Festa-Bianchet, M., J. C. Ray, S. Boutin, S. D. Côté, and A. Gunn. 2011. Conservation of caribou (Rangifer tarandus) in Canada: an uncertain future. Canadian Journal of Zoology 89:419–434.

Finke, J., M. Strein, and M. Sonnenschein. 2008. A simulation framework for modeling anthropogenic disturbances in habitat networks. Ecological Informatics 3:26–34.

Fix, P. J., and A. M. Harrington. 2012. Measuring motivations as a method of mitigating social values conflict. Human Dimensions of Wildlife 17:367–375.

Fullman, T. J., K. Joly, and A. Ackerman. 2017. Effects of environmental features and sport hunting on caribou migration in northwestern Alaska. Movement Ecology 5:4.

Galpern, P., and M. Manseau. 2013. Finding the functional grain: comparing methods for scaling resistance surfaces. Landscape Ecology 28:1269–1281.

Gende, S., A. N. Hendrix, and J. Schmidt. 2018. Somewhere again: migration in freshwater fishes. Canadian Journal of Zoology 86:532–543.

Gesch, D. B. 2007. The national elevation dataset. Pages 99–118 in D. Maune, editor. Digital elevation model technologies and
Martin, S. 2015. Indigenous social and economic adaptations in northern Alaska as measures of resilience. Ecology and Society 20:8.

Mazerolle, M. J. 2019. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.2-2. https://cran.r-project.org/web/packages/AICcmodavg/index.html

McClure, M. L., A. J. Hansen, and R. M. Inman. 2016. Connecting models to movements: testing connectivity model predictions against empirical migration and dispersal data. Landscape Ecology 31:1419–1432.

McRae, B. H., B. G. Dickson, T. H. Keitt, and V. B. Shah. 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724.

Miller, F. L., S. J. Barry, and W. A. Calvert. 2005. Sea-ice crossings by caribou in the south-central Canadian Arctic Archipelago and their ecological importance. Rangifer 16:77–88.

Mowat, G., and D. C. Heard. 2006. Major components of grizzly bear diet across North America. Canadian Journal of Zoology 84:473–489.

Mui, T., R. Serrouya, E. Neilson, H. Li, and S. Boutin. 2015. Influence of in-situ oil sands development on caribou (Rangifer tarandus) movement. PLoS ONE 10:e0136933.

Muir, A. B., B. Caverhill, B. Johnson, M.-J. Fortin, and Y. He. 2017. Using multiple metrics to estimate seasonal landscape connectivity for Blanding’s turtles (Emydoidea blandingii) in a fragmented landscape. Landscape Ecology 32:531–546.

Myers-Smith, I. H., B. K. Arnesen, R. M. Thompson, and F. S. Chapin III. 2006. Cumulative impacts on Alaskan arctic tundra of a quarter century of road dust. Ecoscience 13:503–510.

Mysterud, A., L. E. Loc, B. Zimmermann, R. Bischof, V. Veiberg, and E. Meisingset. 2011. Partial migration in expanding red deer populations at northern latitudes—a role for density dependence? Oikos 120:1817–1825.

Nellemann, C., and G. Fry. 1995. Quantitative analysis of terrain ruggedness in reindeer winter grounds. Arctic 48:172–176.

Nellemann, C., and M. G. Thomsen. 1994. Terrain ruggedness and caribou forage availability during snowmelt on the Arctic Coastal Plain, Alaska. Arctic 47:361–367.

Newton, E. J., B. R. Patterson, M. L. Anderson, A. R. Rodgers, L. M. Vander Venne, and J. M. Fryxell. 2017. Compensatory selection for roads over natural linear features by wolves in northern Ontario: Implications for caribou conservation. PLoS ONE 12:e0186525.

Nielsen, S. E., J. Cranston, and G. B. Stenhouse. 2009. Identiﬁcation of priority areas for grizzly bear conservation and recovery in Alberta, Canada. Journal of Conservation Planning 5:38–60.

Northrup, J. M., M. B. Hooten, C. R. Jr Anderson, and G. Wittmyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. Ecology 94:1456–1463.

Panzacchi, M., B. Van Moorster, and O. Strand. 2013. A road in the middle of one of the last wild reindeer migration routes in Norway: crossing behaviour and threats to conservation. Rangifer 33:15–26.

Parlee, B. L., J. Sandlos, and D. C. Natcher. 2018. Undermining subsistence: Barren-ground caribou in a “tragedy of open access”. Science Advances 4:e1701611.

Paton, D. G., S. Ciuti, M. Quinn, and M. S. Boyce. 2017. Hunting exacerbates the response to human disturbance in large herbivores while migrating through a road network. Ecosphere 8:e01841.

Peterson, G. D., G. S. Cumming, and S. R. Carpenter. 2003. Scenario Planning: a tool for conservation in an uncertain world. Conservation Biology 17:358–366.

Pinard, V., C. Dussault, J.-P. Ouellet, D. Fortin, and R. Courtois. 2012. Calving rate, calf survival rate, and habitat selection of forest-dwelling caribou in a highly managed landscape. Journal of Wildlife Management 76:189–199.

Plante, S., C. Dussault, J. H. Richard, and S. D. Côté. 2018. Human disturbance effects and cumulative habitat loss in endangered migratory caribou. Biological Conservation 224:129–143.

Prokopenko, C. M., M. S. Boyce, and T. Avgar. 2017. Characterizing wildﬁre behavioural responses to roads using integrated step selection analysis. Journal of Applied Ecology 54:470–479.

Quaglia, L., M. Porto, and A. T. Ford. 2019. Simulating animal movements to predict wildlife-vehicle collisions: illustrating an application of the novel R package SiMRiv. European Journal of Wildlife Research 65:100.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Reynolds III, H. V., and G. W. Garner. 1987. Patterns of grizzly bear predation on caribou in Northern Alaska. International Conference on Bear Research and Management 7:59–67.

Sappington, J. M., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71:1419–1426.

Satterthwaite-Phillips, D., C. Krenz, G. Gray, and L. Dodd. 2016. Inunnguit Ililugu Nunampanun: Documenting Our Way of Life Through Maps. Subsistence Mapping Project, Northwest Arctic Borough, Kotzebue, Alaska, USA.

Sawyer, H., N. M. Korfanta, R. M. Nielson, K. L. Monteith, and D. Strickland. 2017. Mule deer and energy development—Long-term trends of habitation and abundance. Global Change Biology 23:4521–4529.

Shah, V., and B. McRae. 2008. Circuitscape: a tool for landscape ecology. Pages 62–65 in G. Varoquaux, Vaught, T., and Millman, J., editors. Proceedings of the 7th Python in Science Conference. Pasadena, California, USA.

Shannon, G., L. M. Angeloni, G. Wittmermyer, K. M. Fristrup, and K. R. Crooks. 2014. Road traffic noise modifies behaviour of a keystone species. Animal Behaviour 94:135–141.

Smith, J. B., Saylor, P. Easton, D. Wiedman, and Elders from the Alaska Villages of Buckland and Deering. 2009. Measurable benefits of traditional food customs in the lives of rural and urban Alaska Inupiaq elders. Alaska Journal of Anthropology 7:89–99.

Southwood, A., and L. Avens. 2010. Physiological, behavioral, and ecological aspects of migration in reptiles. Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology 180:1–23.

Stark, S., M. K. Männistö, and A. Eskelinen. 2015. When do grazers accelerate or decelerate soil carbon and nitrogen cycling in tundra? A test of theory on grazing effects in fertile and infertile habitats. Oikos 124:510–516.

Torres, A., J. A. G. Jaeger, and J. C. Alonso. 2016. Assessing large-scale wildlife responses to human infrastructure development. Proceedings of the National Academy of Sciences USA 113:8472–8477.

Walton, Z., J. Mattisson, J. D. C. Linnell, A. Stien, and J. Odden. 2017. The cost of migratory prey: seasonal changes in semi-domestic reindeer distribution influences breeding success of Eurasian lynx in northern Norway. Oikos 126:642–650.
Whittington, J., M. Hebblewhite, N. J. DeCesare, L. Neufeld, M. Bradley, J. Wilmshurst, and M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. Journal of Applied Ecology 48:1535–1542.

Wilcove, D. S., and M. Wikelski. 2008. Going, going, gone: Is animal migration disappearing? PLoS Biology 6:e188.

Wilson, R. P., I. W. Griffiths, P. A. Legg, M. I. Friswell, O. R. Bidder, L. G. Halsey, S. A. Lambertucci, and E. L. C. Shep ard. 2013a. Turn costs change the value of animal search paths. Ecology Letters 16:1145–1150.

Wilson, R. R., D. D. Gustine, and K. Joly. 2014. Evaluating potential effects of an industrial road on winter habitat of caribou in north-central Alaska. Arctic 67:472–482.

Wilson, R. R., J. R. Liebezeit, and W. M. Loya. 2013b. Accounting for uncertainty in oil and gas development impacts to wildlife in Alaska. Conservation Letters 6:350–358.

Zeller, K. A., K. McGarigal, and A. R. Whiteley. 2012. Estimating landscape resistance to movement: a review. Landscape Ecology 27:777–797.

Ziolkowska, E., K. Ostapowicz, V. C. Radeloff, T. Kuemmerle, A. Sergiel, T. Zwijacz-Kozica, F. Zięba, W. Śmietana, and N. Selva. 2016. Assessing differences in connectivity based on habitat versus movement models for brown bears in the Carpathians. Landscape Ecology 31:1863–1882.

Ziv, G., E. Baran, S. Nam, I. Rodriguez-Iturbe, and S. A. Levin. 2012. Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. Proceedings of the National Academy of Sciences USA 109:5609–5614.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

**Supporting Information**

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2207/full