Received: 22 August 2023 | Accepted: 15 September 2023

DOI: 10.1002/eap.2923

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

ARTICLE

# Effects of vehicle traffic on space use and road crossings of caribou in the Arctic

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**Funding information**
U.S. Geological Survey; U.S. Bureau of Land Management

**Handling Editor:** Paul C. Cross

## Abstract

Assessing the effects of industrial development on wildlife is a key objective of managers and conservation practitioners. However, wildlife responses are often only investigated with respect to the footprint of infrastructure, even though human activity can strongly mediate development impacts. In Arctic Alaska, there is substantial interest in expanding energy development, raising concerns about the potential effects on barren-ground caribou (*Rangifer tarandus granti*). While caribou generally avoid industrial infrastructure, little is known about the role of human activity in moderating their responses, and whether managing activity levels could minimize development effects. To address this uncertainty, we examined the influence of traffic volume on caribou summer space use and road crossings in the Central Arctic Herd within the Kuparuk and Milne Point oil fields on the North Slope of Alaska. We first modeled spatiotemporal variation in hourly traffic volumes across the road system from traffic counter data using gradient-boosted regression trees. We then used generalized additive models to estimate nonlinear step selection functions and road-crossing probabilities from collared female caribou during the post-calving and insect harassment seasons, when they primarily interact with roads. Step selection analyses revealed that caribou selected areas further from roads (~1–3 km) during the post-calving and mosquito seasons and selected areas with lower traffic volumes during all seasons, with selection probabilities peaking when traffic was <5 vehicles/h. Using road-crossing models, we found that caribou were less likely to cross roads during the insect seasons as traffic increased, but that response dissipated as insect harassment became more severe. Past studies suggested that caribou exhibit behavioral responses when traffic exceeds 15 vehicles/h, but our results demonstrate behavioral responses at much lower traffic levels. Our results illustrate that vehicle activity mediates caribou responses to road infrastructure, information that can be used in future land-use planning to minimize the behavioral responses of caribou to industrial development in sensitive Arctic landscapes.

**KEYWORDS**
Arctic, caribou, energy development, habitat selection, infrastructure, movement, *Rangifer tarandus*, road crossing, roads, space use, step selection, traffic

## INTRODUCTION

As industrial development expands across landscapes around the globe, there is a growing need to understand the responses of wildlife to development and to identify effective mitigation strategies to minimize impacts (Butt et al., 2013; Northrup & Wittemyer, 2013; Torres et al., 2016). Industrial development causes habitat loss, fragmentation, and degradation, and while the effects on wildlife can be diverse, they are often deleterious (Fisher & Burton, 2018; van der Ree et al., 2011), inducing changes in animal movements and habitat use patterns (Cristescu et al., 2016; Holloran et al., 2015), altering distributions (Johnson & Russell, 2014), depressing demographic rates (Johnson et al., 2017), and reducing population abundance and density (Benítez-López et al., 2010; Fahrig & Rytwinski, 2009). As a result, wildlife managers and conservation practitioners are highly interested in elucidating the influence of new and existing development on wildlife and identifying practices that effectively reduce its negative impacts (Northrup & Wittemyer, 2013; van der Ree et al., 2011).

Most studies evaluating wildlife responses to human development assess only their reaction to the footprint of infrastructure, even though there is substantial evidence that variation in human activity associated with infrastructure is also strongly influential (Northrup et al., 2012; Shannon et al., 2016; Ware et al., 2015). For example, investigators have found that mule deer more strongly avoid gas wells with greater levels of vehicle traffic (Sawyer et al., 2009), sage grouse exhibit elevated stress hormones when exposed to industrial noise (Blickley, Word, et al., 2012), and blackbirds display advanced reproductive physiology when subjected to nighttime urban lights (Dominoni et al., 2013). Factors such as visual stimulus, noise, and artificial light associated with human activity can have a variety of effects on animals including disrupting behavior, altering breeding and foraging activities, reducing reproductive success, and lowering animal densities (Barber et al., 2010; Davies & Smith, 2018; Lowry et al., 2013; Shannon et al., 2016). While human activity can mediate animal responses to development, measures of human activity are often not readily available and can be difficult to collect, causing most studies to simply investigate responses to the location or density of infrastructure. Understanding the effects of human activity, however, could provide a potential mechanism for mitigation (e.g., temporal or spatial restriction of activity) even in situations where infrastructure remains fixed (Holloran et al., 2015; Northrup & Wittemyer, 2013; Patricelli et al., 2013; Sawyer et al., 2009).

Interest in expanding energy development in the Arctic is raising concerns about the potential effects on wildlife, particularly barren-ground caribou (*Rangifer tarandus*; Fullman, Sullender, et al., 2021; Russell et al., 2021). These migratory caribou are ecologically important as the primary large herbivore in the Arctic, but they are also important culturally, recreationally, and as a key subsistence food resource for Indigenous and rural people (Fall, 2016; Titus et al., 2009). Although barren-ground caribou populations are known to exhibit dramatic population cycles (Bongelli et al., 2020), recent declines in most herds across their range (Russell et al., 2018; Vors & Boyce, 2009) have highlighted the pressures that new development could pose, particularly as the species contends with changing climate conditions (Parlee et al., 2018; Russell et al., 2021). On the North Slope of Alaska, caribou migrate to coastal habitat in the summer to raise their newborn calves, access high-quality forage, and find relief from insects (Griffith et al., 2002; Johnson et al., 2021; White et al., 1975), often using the same areas that are targeted for oil production. Recently there have been proposals for new development projects within the summer ranges of three out of the four Alaskan barren-ground caribou herds (Bureau of Land Management [BLM], 2019, 2020b; Division of Oil and Gas, 2015), renewing interest among wildlife managers in understanding how caribou respond to infrastructure and human activities, and how development impacts can be mitigated.

Barren-ground caribou and conspecific reindeer generally avoid industrial infrastructure (Anttonen et al., 2011; Leblond et al., 2013; Nellemann et al., 2001; Plante et al., 2018; Wilson et al., 2016), a pattern also observed for the Central Arctic Herd (CAH) on the North Slope of Alaska (Cameron et al., 1992; Dau & Cameron, 1986; Johnson et al., 2020; Nellemann & Cameron, 1998; Prichard et al., 2020). During summer, the CAH has the greatest interaction with development of all Alaskan herds in the Arctic, as caribou navigate the Kuparuk, Milne Point, and Prudhoe Bay oil fields to access high-quality forage and insect-relief habitat along the Arctic Ocean (Johnson et al., 2021; White et al., 1975). In response to energy infrastructure, CAH caribou have exhibited avoidance behavior, reduced densities, shifted their calving distributions, and limited their movements (Cameron et al., 1992, 2005; Johnson et al., 2020; Prichard et al., 2020). While the footprint of infrastructure has been associated with altered caribou space use and movement patterns, little is known about the role of human activity in moderating these responses. To maintain caribou movement through the oil fields, environmental plans and impact statements for U.S. federal lands in northern Alaska (e.g., National Petroleum Reserve-Alaska, Arctic National Wildlife Refuge) include stipulations and required operating procedures to reduce vehicle traffic (BLM, 2019, 2020a, 2020b). These documents often state that the impacts on caribou are exacerbated when traffic exceeds 15 vehicles/h (e.g., BLM, 2020a, 2020b), but the underlying evidence for this threshold is limited and based on ground observations of caribou close to roads (e.g., Curatolo & Murphy, 1986; Murphy & Curatolo, 1987), likely inducing bias.

To understand how human activity mediates the responses of barren-ground caribou to energy development, we investigated the space use and movement behavior of females in the CAH relative to vehicle traffic within the Kuparuk and Milne Point oil fields. We assessed responses during three life-history seasons during the summer (post-calving, mosquito harassment, and oestrid fly harassment seasons), during which the majority of CAH interactions with the oil fields occurs (Johnson et al., 2020; Prichard et al., 2020). We first used gradient-boosted machine learning models to predict hourly traffic volumes for road segments across the study area using empirical data from traffic counters. We then used generalized additive models (GAMs) to produce nonlinear step selection functions (SSFs) and road-crossing models to assess the effects of traffic volume on caribou fine-scale summer movements. We hypothesized that caribou would generally avoid roads but would exhibit greater avoidance of roads with higher traffic volumes, likely exhibiting a threshold effect. Additionally, we predicted that the probability of crossing roads would decrease as traffic increased. Finally, we expected that there would be greater avoidance of roads and traffic during the post-calving season, but as insect harassment became more severe during mid to late summer, behavioral responses would wane as caribou became less risk-averse in their need to evade insects (e.g., moving to cooler, windier, less vegetated habitat; Curatolo & Murphy, 1986; Johnson et al., 2021; White et al., 1975).

# METHODS

## Study system

We conducted our study in the Kuparuk and Milne Point oil fields along the coast of the Arctic Ocean on the North Slope of Alaska (Figure 1). Land cover in the region is primarily mesic and wet tundra dominated by graminoids, such as *Cyperaceae* forming tussock tundra and meadows, with scattered ponds, wetlands, rivers, and shrub patches (Gustine et al., 2017; Johnson et al., 2020). The terrain is relatively flat, with gentle slopes facing north toward the Arctic Ocean. The landscape is generally snow free by mid-June, with cooler temperatures and delayed green-up and insect activity phenology near the coast (Johnson et al., 2018, 2021). Mosquitoes (*Culicidae*) become abundant by approximately late June, and warble/bot flies (*Oestridae*) become prominent by approximately mid to late July (Russell et al., 1993; White et al., 1975). Caribou in the CAH generally give birth to their calves south of the oil fields the first week of June and start moving north into the oil fields during the post-calving season (i.e., mid to late June; seasons defined below). During midsummer, caribou are often located within the oil fields adjacent to the coast, primarily to avoid insects and forage on newly emerging vegetation, and then move south out of the oil fields in late July and early August (Johnson et al., 2021; Prichard et al., 2020).

Infrastructure in the Kuparuk and Milne Point oil fields occurs within ~40 km of the coast, with most development within ~20 km of the coast (Figure 1), and consists of a network of gravel roads, pipelines, camps, operational facilities, and well pads. The road system, comprising ~310 km of roads, is closed to the public and is operated primarily by ConocoPhillips Alaska, Inc., in the west, south, and central portions of the study area and by Hilcorp Alaska, LLC, in the northeast. Each company has a main camp serving as their base of operations (ConocoPhillips: central; Hilcorp: northeast; Figure 1). Roads in the oil fields are built on berms above the tundra (~2 m), and pipelines are generally elevated off the ground. Primary roads connecting the main camps, operational facilities, and other road systems total ~95 km in length, while secondary roads connecting the primary roads to well pads are ~215 km in length. Operational facilities include smaller places of operation other than the main camps (e.g., processing, pumping, and minor offices and sleeping quarters). The primary road that runs east–west across the study area (Spine Road) connects the Kuparuk and Milne Point oil fields to other fields (e.g., Prudhoe Bay, Eni) and is seasonally used by North Slope Borough residents. Drivers in the oil fields are instructed to stop when caribou approach the road to facilitate their passage. To assess caribou movements related to roads and traffic, we defined our study area as bounded by the Kuparuk River to the east, the Colville River to the west, the Arctic Ocean to the north, and 10 km (the 99% quantile of caribou movement steps in this analysis) from the nearest road to the south (Figure 1), which encompassed ~2300 km$^2$.

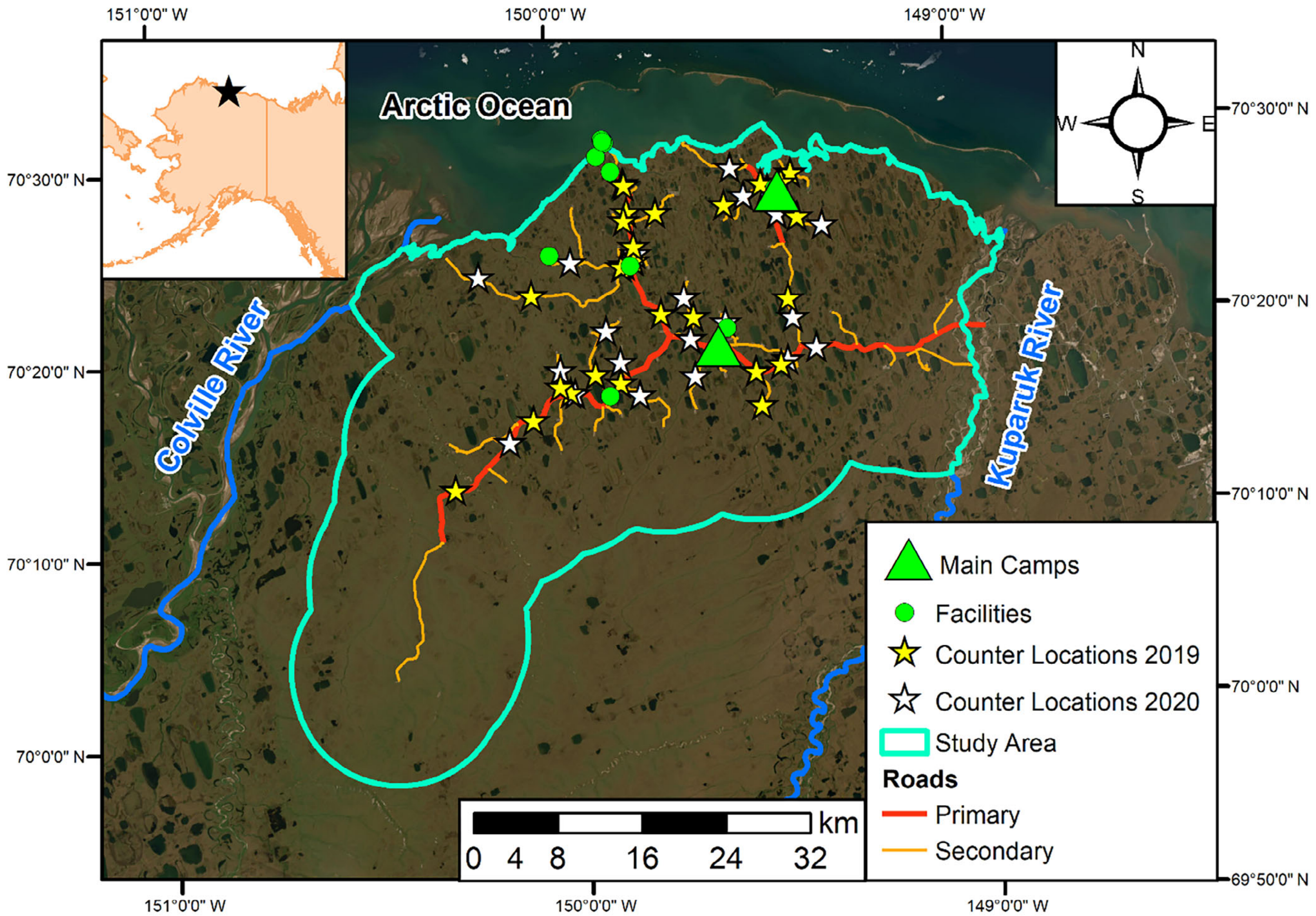


**FIGURE 1** Study area in Kuparuk and Milne Point oil fields used to assess the effect of traffic volume on space use and movements of female caribou in Central Arctic Herd in northern Alaska during summers 2019 and 2020. The study area was bounded by the Colville River, the Kuparuk River, the Arctic Ocean, and 10 km from the roads elsewhere. Traffic counters were randomly placed throughout the road system in both years to monitor hourly traffic volume. The main camps are Hilcorp (north) and ConocoPhillips (central). Facilities include places of operation other than the main camps (e.g., processing, pumping, and minor offices and sleeping quarters).

## Traffic data and prediction model

We monitored traffic in the Kuparuk and Milne Point oil fields during summers 2019 and 2020, starting before caribou regularly used the area and ending after they had generally left. We deployed 25 TRAFx vehicle traffic counters (TRAFx Research Ltd., Canmore, Alberta, Canada) on 12–13 June 2019 and 24 counters on 8–9 June 2020 at random locations throughout the road system representing varying traffic conditions (Figure 1). Counters were placed in waterproof plastic boxes staked securely along the edges of the roads. Locations were changed between 2019 and 2020 to increase spatial coverage of data collection across the road system (Figure 1). The counters recorded traffic volume by measuring changes in the nearby electromagnetic field each time a vehicle moved past a device. Counters were programmed to record the number of vehicles each hour and were recovered from the field on 11 August 2019 and 19 August 2020. We removed the first and the last days of traffic data for each counter to eliminate any spurious counts due to deployment or collection. In 2019, one counter failed completely, and four others did not collect data prior to 28–29 June due to faulty electrical connections. In 2020, two counters were removed during 13–23 July and 22 July–13 August due to road construction, and one other counter collected unreliable data on 24 July when construction vehicles parked nearby (Appendix S1: Figure S1).

While we collected traffic data along a subset of roads in the oil fields, our objective was to predict hourly traffic volumes across the entire road network to associate with locations of caribou fitted with Global Positioning System (GPS) collars. To meet that objective, we first modeled hourly traffic volume from the counters based on several temporal and spatial variables. We split the roads into segments between intersections, given that the traffic volume across each segment should be equivalent (Appendix S1: Figure S2), and then predicted the traffic volume for each segment. Road segments were attributed with the road type (TYPE), with primary roads being major access roads within the oil fields and to the main camps, and secondary roads generally being spur roads from the primary roads to well pads. We also measured the road distance from the counter or road segment to the nearest of the two main camps (ConocoPhillips and Hilcorp camps; CAMPDIST). Similarly, we measured the road distance from the counter or road segment to the nearest facility (main camp or other facility; FACDIST). Lastly, for each counter location and road segment, we determined the number of pads accessible on the road system while going away from the nearest main camp (PADS). This provided an index across the road system of the amount of infrastructure that could be reached from a given location, which we hypothesized would be related to traffic volume.

Using the xgboost package (Chen et al., 2020) in the R environment (R Core Team, 2021), we modeled hourly traffic counts using a Poisson gradient-boosted tree model (Friedman, 2001, 2002; Hastie et al., 2009) as a function of ordinal day (ODAY), year (YEAR), hour of day (HOUR), day of week (WDAY), TYPE, CAMPDIST, FACDIST, and PADS. The trees were grown "leaf-wise" (i.e., best available splits as opposed to a fixed depth) with histogram binning (Ke et al., 2017). To optimize our ability to predict traffic volumes at new locations, we searched a grid of hyperparameters including eta (i.e., learning rate) between 0.001 and 0.3, leaf nodes between 1 and 100, and bagging fraction for each tree between 0.1 and 1 (Friedman, 2002; Hastie et al., 2009). We cross-validated these hyperparameters by withholding each counter in turn, running the model, predicting the hourly counts of the withheld counter, and calculating the root mean squared log error (CV RMSLE), during which the error out to 8000 trees (which exploratory model runs showed was sufficient to find the optimum) was also monitored to determine the optimal number of boosting iterations. The set of hyperparameters that minimized the average CV RMSLE across all counter locations was selected for the final model and was used to predict hourly counts during the monitoring period for each road segment in the study area. To interpret the models, we calculated Shapley additive explanation values (i.e., the additive contribution to the log[count]) to assess variable importance and the effects of the variables on the predictions (Lundberg et al., 2019; Lundberg & Lee, 2017).

## Caribou locations and movements

Between 2016 and 2019, Alaska Department of Fish and Game (ADFG) captured and collared adult female CAH caribou via helicopter net gunning under protocols approved by their agency (Protocol Nos.: 2016-30, 0019-2017-19, 0019-2018-49, 0019-2019-44). Captures occurred in either April or June depending on the year, and caribou were fit with GPS collars (Telonics, Mesa, AZ, USA) programmed to collect a location every 2 h throughout the study period. We selected locations during the same date ranges as the traffic monitoring period described earlier (12 June–11 August 2019; 8 June–19 August 2020) and assigned them to the appropriate summer seasons (i.e., post-calving, mosquito harassment, oestrid fly harassment) based on life history stages for barren-ground caribou (Johnson et al., 2020; Prichard et al., 2020). We defined the post-calving season as 16–24 June, the mosquito harassment season as 25 June–15 July, and the oestrid fly harassment season (which includes some continuing mosquito harassment) as 16 July–7 August.

We considered a caribou step to be the straight-line path between consecutive 2-h fixes. We included all steps that intersected or were contained within a 10-km buffer of the roads in the Kuparuk and Milne Point oil fields (i.e., ~99% quantile of step lengths) and did not cross the Kuparuk or Colville Rivers. We randomly generated 10 available steps for each used step by drawing the step lengths from a gamma distribution estimated with moments, and drawing turning angles from a von Mises distribution estimated with maximum likelihood for turning angle from the used steps for each season (Forester et al., 2009; Panzacchi et al., 2016; Signer et al., 2017). As such, available steps were conditional on the previous location and observed caribou behavior. The available steps met the same boundary conditions as the used steps described earlier, as well as not having an end point in a lake or the ocean.

## Road and habitat covariates

To assess the effects of roads on caribou movements, we attributed the steps (end point for step selection and start point for crossing model) with characteristics including Euclidean distance (in meters) to a road, predicted hourly traffic volume (in vehicles per hour) on the nearest road segment, and road density (in kilometers per square kilometer). We used covariate values at the end points of the steps for the step selection analysis so selected locations were then directly compared to available locations. We used the starting location of road characteristics (distance, traffic, density) for the crossing model, because we expected the animals' perception of the road under the starting conditions would be most likely to affect whether they crossed a road and because average road distance and density along the step would be confounded with crossing events (e.g., distance is 0 where a step crosses a road, and density is generally higher on/near a road). When attributing traffic on the nearest road, we removed spur roads <500 m in length to reduce their influence because they generally occurred near higher-traffic roads. Road density was calculated using the "density.linnet" function with a 500-m bandwidth in the spatstat package (Baddeley et al., 2015) in R to produce a kernel density of the linear network across the study area. We also determined whether each step crossed a road.

In addition to the road and traffic characteristics, we attributed steps with multiple habitat covariates that have been found to influence caribou summer space use (end point for step selection for the same reason described for road covariates and average step conditions for road-crossing models). We used the average of each habitat covariate along each step for the crossing models because we expected the average conditions along the path would be more likely to influence crossing than conditions at discrete start or end points. We acquired 30-m-resolution land-cover data (Boggs et al., 2016; https://accscatalog.uaa.alaska.edu/node/41/revisions/80/view), which included herbaceous (mesic herbaceous), wet herbaceous (marsh, wet marsh), barren (bare ground, sparsely vegetated), tussock tundra, open water (coastal, freshwater), and low shrub (low shrub, dwarf shrub) categories, and we averaged the cover of each category within 500-m-radius moving windows to attribute to the steps. We also attributed each step with terrain ruggedness, topographic position, and aspect (Johnson et al., 2020, 2021; Severson et al., 2021) derived from a 30-m-resolution digital elevation model (U.S. Geological Survey [USGS] National Elevation Dataset; https://www.usgs.gov/the-national-map-data-delivery). Additionally, we measured distance from perennial streams (https://www.usgs.gov/national-hydrography).

Lastly, to quantify the effects of insect harassment, we attributed caribou steps with an hourly mosquito index and oestrid fly index based on the insect activity formulae in Russell et al. (1993). The indices were calculated for caribou locations (end point for step selection and average step conditions for road-crossing models) based on the spatial coordinates, date, and time using spatial hourly temperature and wind speed data from ERA5 (Muñoz Sabater, 2019; 0.1° resolution). Biting and parasitic insects are generally not abundant during the post-calving season but can be a primary driver of caribou movements during the midsummer mosquito harassment season (Johnson et al., 2021; White et al., 1975) and may also influence movements during the later oestrid fly harassment season (Wilson et al., 2012), and we used those specific indices (mosquito and oestrid) in their respective seasons.

## Step selection models

To assess caribou habitat selection in response to roads and traffic, we conducted a SSF analysis (Fortin et al., 2005; Thurfjell et al., 2014), where we used conditional logistic regression within a GAM framework (Wood, 2017). We chose a GAM approach to allow nonlinear responses and to facilitate the identification of threshold values. For each summer season (i.e., post-calving, mosquito harassment, oestrid fly harassment) we ran a single global model (Fieberg & Johnson, 2015) that included covariates related to our hypotheses (i.e., traffic volume, road distance, insect harassment), along with those covariates known to influence caribou space use (e.g., related to land cover, topography). Results from season-specific global models were then used to assess our hypotheses about caribou behavioral responses to roads and traffic.

Each season-specific model was run using the "gam" function with the "cox.ph" family in the mgcv package (Wood, 2017) in R version 4.1.2 (R Core Team, 2021), where each used step and its paired available steps were conditional strata. To better estimate habitat effects, we included the log of the step lengths (because movement rates can be faster near roads; Boulanger et al., 2020; Leblond et al., 2013; Prichard et al., 2020) and the cosine of the turning angles, thereby making the analysis an integrated SSF (Avgar et al., 2016). We first assessed all covariates for multicollinearity using variance inflation factors (VIFs) and correlation coefficients (VIF > 5 and $|r| > 0.6$; Legendre & Legendre, 2012; Zuur et al., 2009). Only herbaceous and wet herbaceous habitats were correlated ($r = -0.81$), and we removed herbaceous habitats due to a higher Akaike's information criterion value (Burnham & Anderson, 2002; Dormann et al., 2013) in a univariate SSF calculated for all seasons.

We produced season-specific models using the habitat covariates (i.e., related to land cover, topography, and distance to river) described earlier, in addition to road and traffic effects (Prokopenko et al., 2017; Scrafford et al., 2018). To control for the large-scale spatial configuration of the road system in the study area, which was not evenly distributed (Figure 1), we also included a covariate for road density. The models included a cubic regression cyclic spline for aspect to account for the circular distribution and thin plate regression shrinkage splines with a null space penalty for all other covariates (Wood, 2017).

The shrinkage splines allowed the effective degrees of freedom (edf) to shrink to 1 (i.e., linear) or toward 0 (i.e., no effect) as appropriate due to the null space penalty (Wood, 2017). We set the maximum knots to four to limit overfitting but still allow for quadratic-like effects. We also included a spatial autocorrelation term to help account for missing covariates using a Gaussian process smoothing basis with the spatial covariance function and range parameter suggested by Kammann and Wand (2003) and Wood (2017).

To assess our hypotheses related to road and traffic effects, we included road distance and traffic volume in each season-specific model. We hypothesized that caribou would avoid roads and exhibit greater avoidance of roads with higher traffic, and thus we evaluated a traffic × road distance interaction. We used a traffic × road distance interaction because we expected road distance to mediate the influence of traffic on caribou (Scrafford et al., 2018) as traffic effects would likely diminish with distance. We included interactions as tensor product smooths to account for the different scales of the covariates (Wood, 2017). Additionally, we hypothesized that insect harassment would reduce avoidance of roads and traffic as caribou are highly motivated to move to areas with lower insect activity (Curatolo & Murphy, 1986; Johnson et al., 2021; Smith & Cameron, 1985). To test this hypothesis, during each insect season, we included the insect activity index in the interaction to produce a three-way interaction: traffic × road distance × insect index. We plotted and interpreted variables with $p < 0.15$ and displayed response plots with 85% CIs (Arnold, 2010).

To produce response plots, we averaged the response across the naturally occurring combinations of available values and used GAMs to plot the response of the predicted availability values against the variables of interest (Avgar et al., 2017; Mancinelli et al., 2019). The effects were plotted as $e^{logit}/(1 + e^{logit})$, where "logit" is the linear predictor of the model (Fieberg et al., 2021). To account for the estimated variation in the model, we calculated the CIs of the average responses by fitting GAMs to the upper and lower bounds of the 85% CI of the model predictions. Additionally, in these response plots, to aid interpretation of the interactions, we also estimated the responses for different levels of traffic volume and road distance.

## Road-crossing models

We used logistic regression to isolate the effects of traffic volume on the probability a caribou would cross a road (Gagnon et al., 2007). Similar to the SSF analysis, we built a single global model for each season, comparing used steps that crossed roads with those that did not. We used GAMs to allow nonlinear responses and identify potential threshold values. Models included general habitat covariates known to influence caribou movement (i.e., related to land cover, topography, and distance to river) and those specifically related to our hypotheses (i.e., road distance, traffic, and insect indices).

GAMs were run with the mgcv package in R using the "binomial" family. A random intercept for each individual-year was included to account for potentially correlated steps for each individual. We also included the length of the movement step and road density as controlling factors because they can affect crossing probability (e.g., longer movements are more likely to cross a road; if there are more roads nearby, a caribou is more likely to cross a road). Similar to the SSF models, aspect was fit with a cubic regression cyclic spline, and the other covariates (i.e., related to habitat, road distance, traffic, and insect conditions) were fit with shrinkage splines with a null space penalty and a maximum number of four knots (Wood, 2017). Covariates were screened for multicollinearity, similar to the SSF analysis, and herbaceous habitat was removed.

To assess road and traffic effects, we included road distance and traffic along with the habitat covariates described previously (same as those in the SSF analysis). We used a traffic × road distance interaction in the post-calving season model, and to assess the mediating role of insects, we used a traffic × road distance × insect index three-way interaction in the models for the mosquito harassment and oestrid fly harassment seasons. We expected that road distance would primarily be a nuisance variable, with road distance inversely related to road-crossing probability, and that it would also have a mediating effect on traffic volume because traffic should have a stronger effect when caribou are closer to roads. We plotted and interpreted covariates with $p < 0.15$ and displayed response plots with 85% CIs (Arnold, 2010), similar to the SSF analysis. Because road distance was a nuisance variable in our crossing models (i.e., caribou must approach a road to cross it, but the distance to a road is arbitrarily determined by when the GPS unit records the location), to generate predicted effects for interpretation, we fixed the prediction distance to 50 m to represent a caribou approaching a road.

# RESULTS

## Traffic predictions

We acquired traffic data from 48 monitoring locations throughout the Kuparuk and Milne Point road systems across the 2 years of our study. In 2019, the average hourly vehicle counts at the different counter sites ranged from 1.4 to 35.4, with a mean of 12.4 vehicles/h, and in 2020 they ranged from 0.2 to 43.8, with a mean of 8.3 vehicles/h. Overall, traffic was generally less in 2020, due to reduced oil field activity during the COVID-19 pandemic.

For the traffic prediction model, the selected set of hyperparameters included a shrinkage rate of 0.2, four leaves/tree, bagging fraction of 1, and 5880 trees, and the CV RMSLE error was 0.80 (CV RMSE = 7.86; $R^2 = 85.1\%$). The most important variable in predicting traffic volume was PADS followed by HOUR, CAMPDIST, TYPE, YEAR, and FACDIST (Appendix S1: Figure S3). Traffic volume increased with an increasing number of accessible pads and closer to the main camps and facilities (Figure 2a, Appendix S1: Figure S4). Additionally, traffic volume was greater during midday (07:00 to 17:00) than at night, greater in 2019 than 2020, and greater on primary roads than secondary roads (Figure 2a, Appendix S1: Figure S4). Ordinal day and day of the week had low importance and did not display clear effects (Appendix S1: Figure S4).

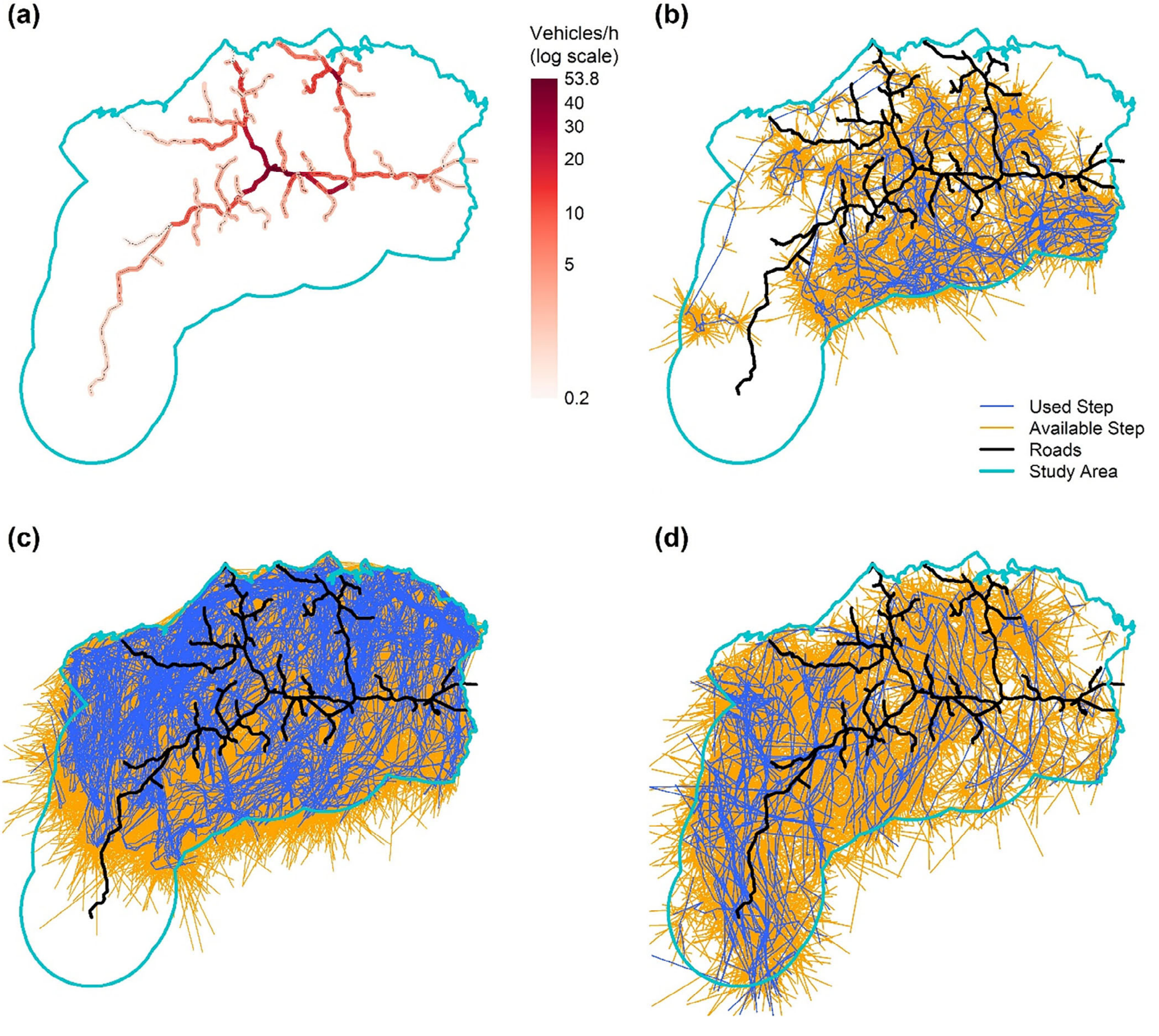


**FIGURE 2** Study area boundary in Kuparuk and Milne Point oil fields showing (a) predicted average hourly vehicle traffic volume across road system, and caribou steps and available steps (1:10 used to available ratio) during the (b) post-calving season (used steps $n = 2615$), (c) mosquito harassment season (used steps $n = 11{,}215$), and (d) oestrid fly harassment season (used steps $n = 2495$), summers 2019 and 2020. The study area was between the Colville and Kuparuk Rivers, south of the Arctic Ocean, and within 10 km of roads. Caribou steps that intersected the boundary were included in the analysis, and available steps were allowed to go outside the boundary to limit availability bias (but were not allowed to cross the rivers or go into the ocean).

## Caribou data

We collected locations from 48 female caribou during our study period, resulting in 115 individual-years, of which 79 occurred within our study area, representing 47.6% of all locations. During the post-calving, mosquito harassment, and oestrid fly harassment seasons, 44.8%, 62.3%, and 25.8% of all locations, respectively, occurred within our study area. A total of 16,334 caribou steps in the study period met our requirements for inclusion in the analysis, of which 16.0%, 68.7%, and 15.3% occurred in each season (Figure 2b–d) representing 63, 77, and 73 individual-years, respectively. The mean 2-h step length was 1669 m overall and 891, 1818, and 1947 m during the post-calving, mosquito harassment, and oestrid fly harassment seasons, respectively. The insect activity indices were relatively low during our study period, with ~1% of locations during the mosquito season and ~5% of locations during the oestrid fly season experiencing high insect activity (>0.4; Prichard et al., 2020).

## Step selection models

In the SSF models for all summer seasons, wet herbaceous habitat, topographic position index, aspect, and terrain ruggedness were important in explaining caribou space use ($p < 0.15$; Table 1). Caribou generally selected areas with less wet herbaceous habitat, for "ridge" topography, and more rugged terrain, while they selected southwest aspects during the post-calving season and northern aspects during the mosquito and oestrid fly seasons (Appendix S1: Figure S5). Additionally, during the post-calving and mosquito harassment seasons, caribou selected areas with more tussock tundra habitat, less water, and lower road densities, with a stronger response during the post-calving season (Figure 3). The influence of road density was effectively removed from the oestrid harassment season model by the shrinkage splines (Table 1). During the mosquito harassment season, caribou also selected for less barren habitat, less low shrub habitat, and areas closer to rivers. During the oestrid fly harassment season, caribou additionally selected for areas with some barren habitat, more low shrub habitat, and areas closer to rivers.

Related to our hypotheses, the traffic × road distance interaction was significant ($p = 0.025$) in the post-calving model (Table 1). Caribou generally selected areas >3 km from roads and with lower traffic (Figure 4a,b). The strongest effect of traffic was at low traffic levels far from roads, because, due to the road configuration, there were few areas far from roads with high traffic volume (Figure 4a). Additionally, because caribou strongly selected areas further from roads during this season, there were relatively little data at near and intermediate distances from roads (i.e., within ~2.5 km), and responses to traffic within those distances showed no clear effect (Figure 4b). During the mosquito harassment season, the traffic × road distance × mosquito index three-way interaction was significant ($p < 0.001$; Table 1). Habitat selection generally increased ~1–2 km from roads, and caribou selected for low traffic volume (Figure 4d,e), with the highest probabilities of use occurring at <3 vehicles/h (Figure 4e). Areas with high mosquito activity were strongly avoided at all traffic volumes (Figure 4f). During the oestrid fly harassment season, there was no support for the three-way interaction (traffic × road distance × oestrid fly index; $p = 0.323$), but there was support for all two-way interactions (traffic × road distance, road distance × oestrid fly index, and traffic × oestrid fly index; Table 1; $p \leq 0.145$). There was little discernible response to road distance (Figure 4g), but caribou generally had higher probabilities of selecting areas with very low traffic (~1–3 vehicles/h; Figure 4h), generally using the western portion of the study area that had lower traffic volumes (Figure 2d). Caribou also generally avoided areas predicted to have high oestrid fly activity (Figure 4i).

## Road crossing models

During the post-calving, mosquito harassment, and oestrid fly harassment seasons, 3.0% ($n = 79$ of 2593), 12.8% ($n = 1464$ of 11,478), and 12.3% ($n = 314$ of 2555) of the caribou steps within our study area crossed a road, respectively. The global models explained 66.2%, 51.1%, and 52.8% of the deviance in caribou crossings for the post-calving, mosquito harassment, and oestrid fly harassment seasons, respectively. As expected, step length and road density were important in determining crossing probabilities in all three seasons, with longer-distance movements and closer roads leading to a higher probability of crossing (Table 2; Appendix S1: Figure S6). Barren habitat was also important in all three seasons, with crossing probability peaking when habitat was 15%–40% barren (Table 2; Appendix S1: Figure S6). Additionally, crossing increased with greater proportions of wet herbaceous habitat in the post-calving and oestrid seasons and with greater proportions of low shrub habitat during the oestrid season, but crossings decreased with greater proportions of water in the mosquito season. Crossings declined with greater terrain ruggedness during the mosquito and oestrid seasons, but increased further from rivers during the post-calving season and at intermediate distances from rivers during the mosquito season (Table 2; Appendix S1: Figure S6).

**TABLE 1** Results from global generalized additive models of female caribou habitat selection during post-calving, mosquito harassment, and oestrid fly harassment seasons in the Kuparuk and Milne Point oil fields, Alaska, during 2019–2020.

| Season | Covariate | edf | *p*-value |
|---|---|---|---|
| Post-calving | **Wet herbaceous** | **1.291** | **<0.001** |
| | Barren | 0.006 | 0.795 |
| | **Tussock** | **0.835** | **0.015** |
| | **Water** | **0.956** | **<0.001** |
| | Low shrub | 0.004 | 0.470 |
| | **Topographic position** | **0.967** | **<0.001** |
| | **Aspect** | **1.841** | **<0.001** |
| | **Terrain ruggedness** | **0.974** | **<0.001** |
| | Distance to river | 0.005 | 0.695 |
| | **Road density** | **0.946** | **<0.001** |
| | **Traffic × Road.Distance** | **1.381** | **0.025** |
| | Traffic | 0.005 | 0.608 |
| | **Road.Distance** | **2.401** | **<0.001** |
| | **Spatial autocorrelation** | **10.229** | **<0.001** |
| | **Log (Step.Length)** | **2.807** | **<0.001** |
| | **Cos (Turn.Angle)** | **2.664** | **<0.001** |
| Mosquito harassment | **Wet herbaceous** | **2.636** | **<0.001** |
| | **Barren** | **0.679** | **0.076** |
| | **Tussock** | **0.909** | **0.001** |
| | **Water** | **1.035** | **<0.001** |
| | **Low shrub** | **0.593** | **0.115** |
| | **Topographic position** | **0.992** | **<0.001** |
| | **Aspect** | **1.601** | **0.001** |
| | **Terrain ruggedness** | **0.978** | **<0.001** |
| | **Distance to river** | **2.860** | **<0.001** |
| | **Road density** | **0.930** | **0.001** |
| | **Traffic × Road.Distance × Mosquito** | **7.550** | **<0.001** |
| | **Traffic × Road.Distance** | **0.499** | **0.149** |
| | **Traffic × Mosquito** | **2.397** | **0.003** |
| | **Road.Distance × Mosquito** | **6.047** | **<0.001** |
| | Traffic | 0.078 | 0.351 |
| | **Road.Distance** | **1.018** | **0.003** |
| | **Mosquito** | **1.566** | **<0.001** |
| | **Spatial autocorelation** | **13.084** | **<0.001** |
| | **Log (Step.Length)** | **2.896** | **<0.001** |
| | **Cos (Turn.Angle)** | **2.964** | **<0.001** |
| Oestrid fly harassment | **Wet herbaceous** | **2.116** | **<0.001** |
| | **Barren** | **2.377** | **<0.001** |
| | Tussock | 0.471 | 0.161 |
| | Water | 0.003 | 0.920 |
| | **Low shrub** | **0.774** | **0.033** |
| | **Topographic position** | **0.885** | **0.004** |

**TABLE 1** (Continued)

| Season | Covariate | edf | *p*-value |
|---|---|---|---|
| | **Aspect** | **0.865** | **0.141** |
| | **Terrain ruggedness** | **1.922** | **<0.001** |
| | **Distance to river** | **2.669** | **<0.001** |
| | Road density | 0.004 | 0.927 |
| | Traffic × Road.Distance × Oestrid | 0.084 | 0.323 |
| | **Traffic × Road.Distance** | **0.549** | **0.145** |
| | **Traffic × Oestrid** | **1.045** | **0.007** |
| | **Road.Distance × Oestrid** | **2.936** | **<0.001** |
| | Traffic | 0.008 | 0.538 |
| | Road.Distance | 0.021 | 0.179 |
| | **Oestrid** | **2.224** | **<0.001** |
| | **Spatial autocorrelation** | **7.814** | **0.001** |
| | **Log (Step.Length)** | **2.140** | **<0.001** |
| | **Cos (Turn.Angle)** | **2.937** | **<0.001** |

*Note*: Covariates with a $p < 0.15$ are in bold and plotted in Appendix S1.
Abbreviation: edf, effective degrees of freedom.

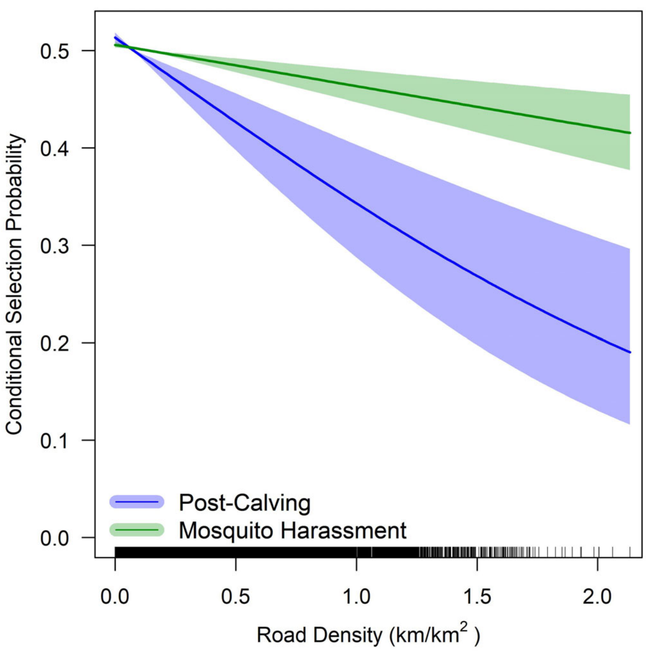


**FIGURE 3** Conditional probability of selection (±85% CI) of female caribou for road density during the post-calving and mosquito harassment seasons in the Kuparuk and Milne Point oil fields, Alaska, during 2019–2020.

Based on the global road-crossing model for the post-calving season, we found there was no support for traffic in explaining caribou road crossings (Table 2). We suspect that the low number of crossing events during this season ($n = 79$) may have inhibited our ability to assess multiple covariates and the interaction term. During the mosquito harassment season, the traffic × road distance × mosquito three-way interaction was significant ($p < 0.001$; Table 2). When mosquito harassment was low, caribou were most likely to cross roads at lower traffic levels (Figure 5a), but as harassment increased and caribou sought relief from insects, their response to traffic dissipated, and they were more likely to cross roads at intermediate traffic volumes (Figure 5b). Given limited data for when mosquito harassment and traffic levels were both high, there was significant uncertainty in caribou responses under such conditions. During the oestrid fly harassment season, the traffic × road distance × oestrid interaction was also supported ($p = 0.051$; Table 2). The interaction showed a similar response to the mosquito harassment season, with caribou more likely to cross roads at lower traffic levels when oestrid fly harassment was low (Figure 5a) and the response dissipating as harassment increased (Figure 5c).

## DISCUSSION

Assessing the effects of human development on wildlife is a key objective of managers and conservation practitioners, but wildlife responses are often only investigated with respect to the footprint of infrastructure, even though human activity can strongly mediate development impacts (Fahrig & Rytwinski, 2009; Northrup &

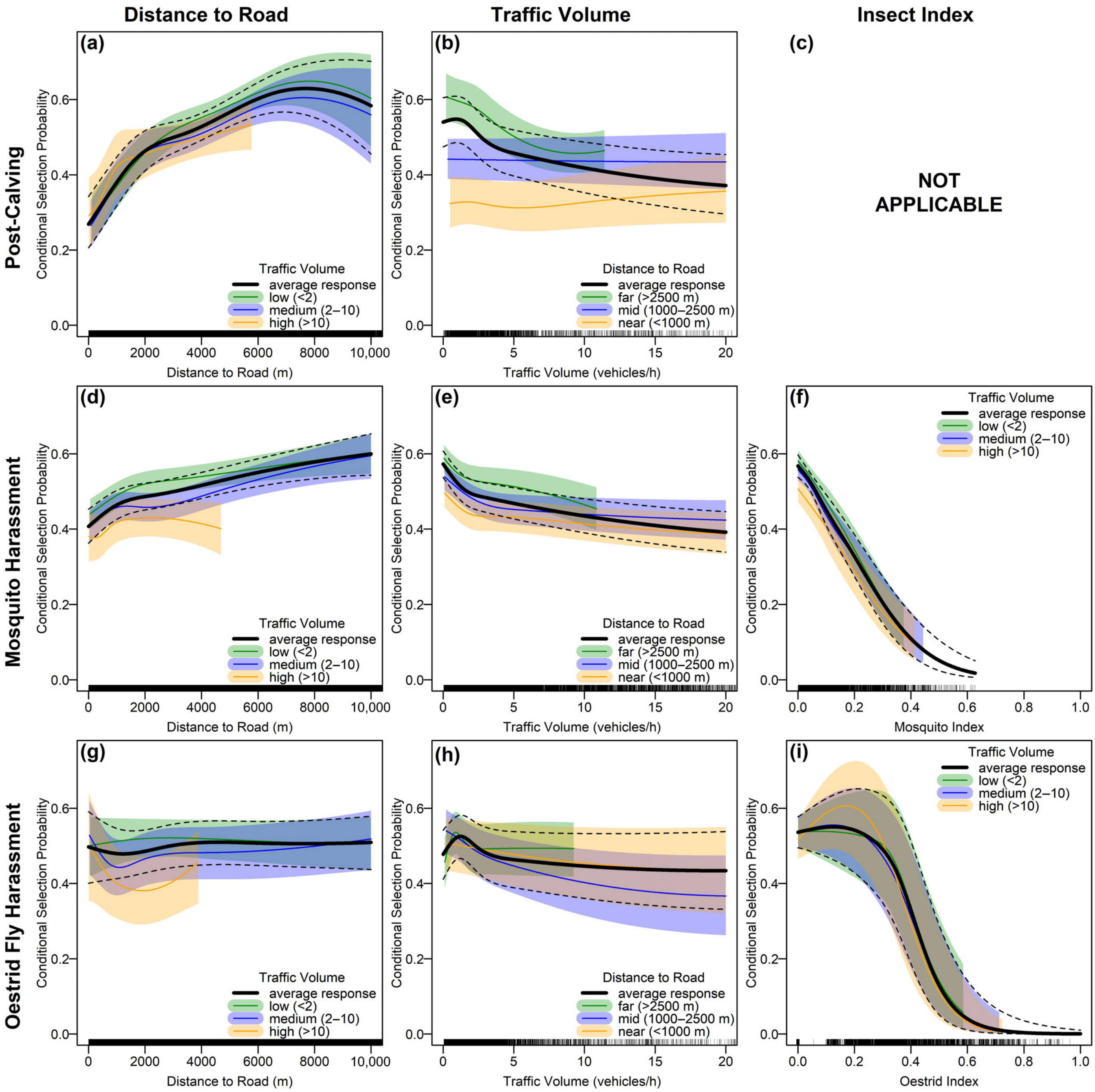


**FIGURE 4** Conditional probabilities of selection (±85% CIs) of female caribou for road distance, traffic, and insect conditions during summer in the Kuparuk and Milne Point oil fields, Alaska, during 2019–2020. The rows depict responses by caribou from step selection models in different summer seasons (post-calving, mosquito harassment, oestrid fly harassment, respectively), and the columns are the three main variables assessed (road distance, traffic volume, and insect index). Insect index was not included in the post-calving season model (not applicable). The bold black line is the overall average response, and the dashed black lines represent the overall 85% CIs. The colored lines split out the responses into different levels of other variables to aid in the interpretation of the interactions. The response curves are truncated at the 99% quantile of values for that level.

Wittemyer, 2013; Wisdom et al., 2018). By investigating the responses of barren-ground caribou to both road infrastructure and traffic levels, we found that caribou reduced their space use near roads during the post-calving and mosquito harassment seasons but reduced their space use near high-traffic roads in all seasons. Although we used GAMs to determine whether caribou responses to traffic volume exhibited threshold effects, we instead found that the probability of a caribou crossing a road generally declined as a continuous function of

**TABLE 2** Results from global generalized additive models of the probability of female caribou crossing a road during the post-calving, mosquito harassment, and oestrid fly harassment seasons in the Kuparuk and Milne Point oil fields, Alaska, during 2019–2020.

| Season | Covariate | edf | *p*-value |
|---|---|---|---|
| Post-calving | **Wet herbaceous** | **1.764** | **0.008** |
| | **Barren** | **1.997** | **<0.001** |
| | Tussock | 0.000 | 0.392 |
| | Water | 0.000 | 0.690 |
| | Low shrub | 0.000 | 0.723 |
| | Topographic position | 0.402 | 0.226 |
| | Aspect | 0.533 | 0.232 |
| | Terrain ruggedness | 0.000 | 0.967 |
| | **Distance to river** | **0.557** | **0.134** |
| | **Road density** | **0.882** | **0.003** |
| | Traffic × Road.Distance | 0.000 | 0.849 |
| | Traffic | 0.000 | 0.872 |
| | **Road.Distance** | **1.296** | **<0.001** |
| | **Log (Step.Length)** | **1.023** | **<0.001** |
| Mosquito harassment | Wet herbaceous | 0.000 | 0.517 |
| | **Barren** | **2.974** | **<0.001** |
| | Tussock | 0.533 | 0.172 |
| | **Water** | **1.694** | **0.000** |
| | Low shrub | 0.000 | 0.448 |
| | Topographic position | 0.000 | 0.707 |
| | Aspect | 0.000 | 0.821 |
| | **Terrain ruggedness** | **0.804** | **0.024** |
| | **Distance to river** | **2.212** | **<0.001** |
| | **Road density** | **1.645** | **<0.001** |
| | **Traffic × Road.Distance × Mosquito** | **3.934** | **0.001** |
| | **Traffic × Road.Distance** | **1.708** | **<0.001** |
| | Traffic × Mosquito | 0.000 | 0.532 |
| | **Road.Distance × Mosquito** | **4.817** | **<0.001** |
| | **Traffic** | **0.537** | **0.041** |
| | **Road.Distance** | **1.909** | **<0.001** |
| | **Mosquito** | **1.069** | **<0.001** |
| | **Log (Step.Length)** | **2.958** | **<0.001** |
| Oestrid fly harassment | **Wet herbaceous** | **0.882** | **0.013** |
| | **Barren** | **2.904** | **<0.001** |
| | Tussock | 0.000 | 0.552 |
| | Water | 0.000 | 0.915 |
| | **Low shrub** | **0.857** | **0.007** |
| | Topographic position | 0.000 | 0.553 |
| | Aspect | 0.000 | 0.481 |
| | **Terrain ruggedness** | **0.933** | **0.001** |
| | Distance to river | 0.473 | 0.161 |
| | **Road density** | **1.115** | **<0.001** |

(Continues)

**TABLE 2** (Continued)

| Season | Covariate | edf | $p$-value |
|---|---|---|---|
| | **Traffic × Road.Distance × Oestrid** | **1.850** | **0.051** |
| | **Traffic × Road.Distance** | **1.581** | **0.007** |
| | **Traffic × Oestrid** | **0.634** | **0.100** |
| | **Road.Distance × Oestrid** | **0.862** | **0.040** |
| | Traffic | 0.000 | 0.193 |
| | **Road.Distance** | **1.426** | **<0.001** |
| | **Oestrid** | **1.982** | **0.010** |
| | **Log (Step.Length)** | **2.809** | **<0.001** |

*Note*: Covariates with a $p < 0.15$ are in bold and plotted in Appendix S1.
Abbreviation: edf, effective degrees of freedom.

increasing traffic, except during high insect activity, and that caribou displayed responses in their space use even at levels well below (~0–5 vehicles/h) what was previously suggested as a threshold (15 vehicles/h; Curatolo & Murphy, 1986; Murphy & Curatolo, 1987; Murphy & Lawhead, 2000). As a result, roads, particularly with higher traffic volumes, were found to reduce caribou movements and their use of preferred summer habitats. Our results demonstrate that spatiotemporal variation in human activity can have important effects on caribou behavior, information that can be used to identify potential mitigation strategies for minimizing impacts from existing and planned infrastructure.

Our findings on caribou responses to road infrastructure largely corroborate other studies on caribou and conspecific reindeer (Anttonen et al., 2011; Leblond et al., 2013; Nellemann et al., 2001). For example, during the post-calving and mosquito harassment periods, our results substantiate the finding of previous studies on the CAH within oil fields that caribou generally reduce their use of habitat within ~1–3 km of roads (Cameron et al., 1992; Dau & Cameron, 1986; Johnson et al., 2020; Prichard et al., 2022). Given that this pattern has now been detected using a variety of analytical methods over ~40 years, it suggests that the observed impacts are consistent and robust. In Europe, reindeer have been similarly observed to avoid infrastructure and roads for ~2–3 km during both summer and winter (Anttonen et al., 2011; Nellemann et al., 2001; Skarin et al., 2015). While some investigators have reported much larger avoidance distances (e.g., ≥6 km; Boulanger et al., 2020; Fullman, Wilson, et al., 2021; Johnson & Russell, 2014), their studies analyzed large landscape-scale responses as opposed to finer-scale movement behaviors, which may account for some of the discrepancies. Additionally, we found that caribou use of habitat declined as road density increased to ~2 km/km$^2$ (the maximum observed value in our study area) during the post-calving and mosquito harassment seasons. Nellemann and Cameron (1998) similarly observed lower caribou densities at higher road densities, with caribou density declining by 86% with >0.9 km road/km$^2$, while Vistnes et al. (2001) reported complete abandonment of habitat by reindeer when linear features exceeded 1.3 km/km$^2$. While our results did not indicate road density threshold effects, it is important to recognize that in our study system, caribou must cross roads to access key summer habitat (Johnson et al., 2020, 2021), so they may have more limited ability to abandon or circumnavigate developed areas. Additionally, within the oil fields we investigated, drivers are instructed to stop when caribou approach roads. We suspect caribou responses to vehicles may be stronger in areas where drivers do not routinely slow and stop.

Importantly, while we found that the road footprint influenced caribou behavior, we also found that traffic volume mediated caribou responses to roads. Although caribou in our study area routinely crossed roads (3.0%, 12.8%, and 12.3% of steps within our study area crossed roads during the post-calving, mosquito, and oestrid seasons, respectively), they were more likely to cross roads during the insect seasons when there were lower traffic volumes (Figure 5a). We suspect this pattern may also hold during the post-calving season, but limited observations of crossings ($n = 79$) likely reduced our ability to parameterize more complex models. Additionally, during the insect harassment seasons, caribou habitat selection probabilities peaked at traffic volumes less than 5 vehicles/h. Notably, this is well below the threshold of 15 vehicles/h that was identified as inhibiting CAH caribou movements in past studies (Curatolo & Murphy, 1986; Murphy & Curatolo, 1987; Murphy & Lawhead, 2000) and that has been used to describe caribou responses to traffic in several recent government environmental assessments (e.g., BLM, 2019, 2020a, 2020b). Past

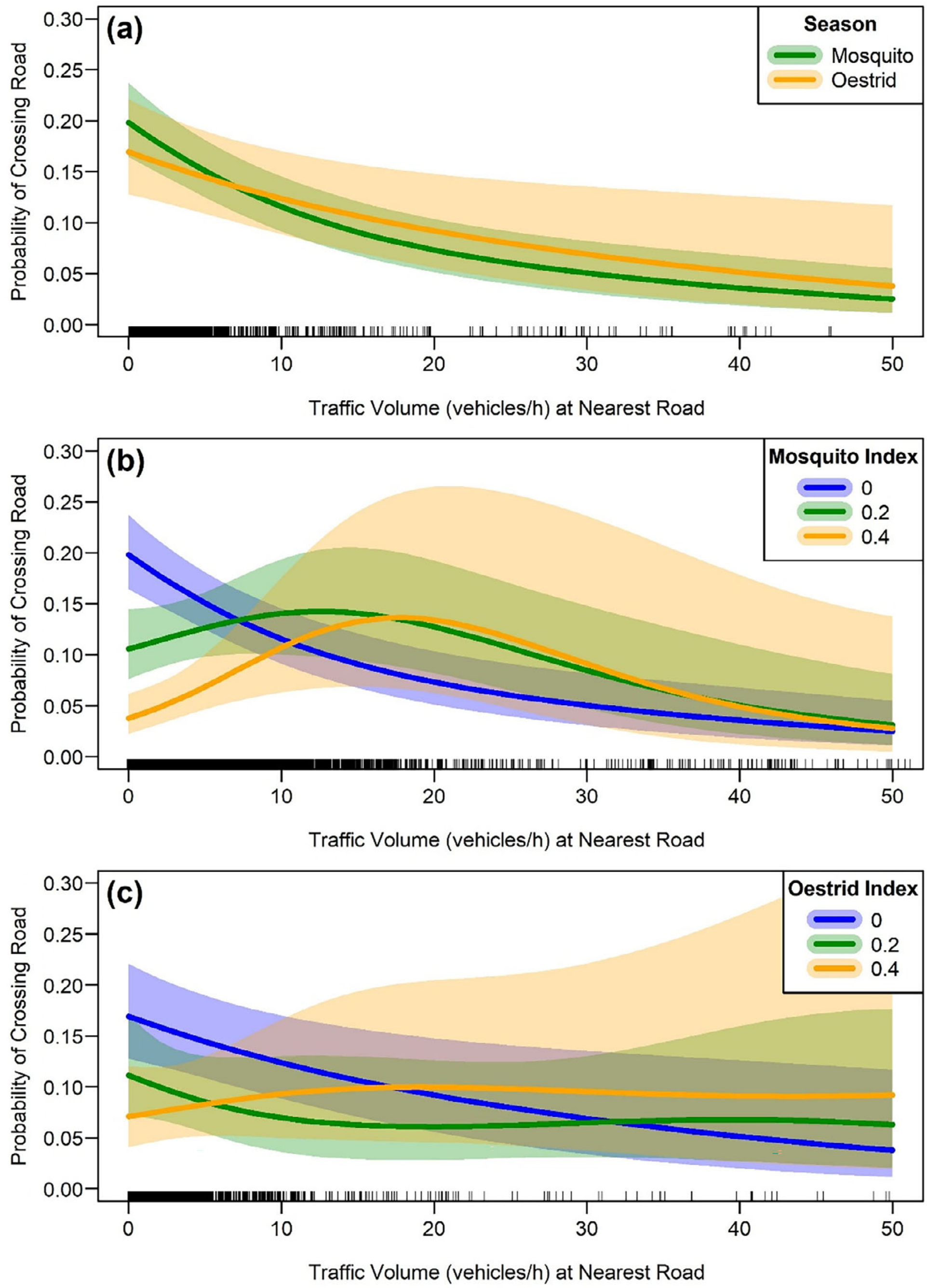


**FIGURE 5** Probabilities (±85% CIs) of female caribou crossing a road during different summer seasons (post-calving, mosquito harassment, and oestrid fly harassment) in the Kuparuk and Milne Point oil fields as function of traffic volume at nearest road, Alaska, 2019–2020. (a) Effect of traffic on the probability of caribou crossing a road during insect seasons when there is no harassment. (b) Interaction between traffic and mosquito index during the mosquito harassment season. (c) Interaction between traffic and oestrid fly index during the oestrid fly harassment season. In both models, because distance was included as a nuisance-controlling variable, the probability of crossing was calculated as caribou approach a road (i.e., 50 m).

published studies on traffic effects in the Kuparuk oil field (Curatolo & Murphy, 1986; Murphy & Curatolo, 1987) occurred in the 1980s before widespread use of fine-scale animal tracking devices and were therefore based on visual surveys from roads, which caribou generally avoid. Additionally, these studies only compared caribou behavioral responses in areas near a pipeline and road with high traffic (~15 vehicles/h), a pipeline and road with low traffic (<1 vehicle/h), and without development, providing limited inferences about the responses of caribou to variation in traffic volume. Other species of ungulates and carnivores have also exhibited negative behavioral responses to similarly low levels of traffic (<5 vehicles/h), with reduced road crossing and changes in habitat use behavior (Ciuti et al., 2012; Northrup et al., 2012; Scrafford et al., 2018; Wilson et al., 2016).

While caribou generally selected for lower traffic levels, their responses to traffic were also strongly modulated by insect harassment. At low levels of insect harassment, caribou were more likely to cross roads with lower levels of traffic (Figure 5a), but when insect harassment increased, this effect dissipated (Figure 5b,c). Because high insect activity (>0.4; Prichard et al., 2020) was infrequent during the insect harassment seasons in our study period, there was greater uncertainty in caribou responses under those conditions. That said, our findings generally corroborate patterns observed from previous studies (Curatolo & Murphy, 1986; Murphy & Curatolo, 1987; Prichard et al., 2020), finding that caribou responses to infrastructure dampened, and road crossings increased, with greater insect harassment. As harassment increases in severity, we suspect that caribou cannot afford to be strongly risk averse with respect to roads and traffic (Frid & Dill, 2002), as they must travel to areas with cooler, windier weather to evade insects. Avoidance of human infrastructure by black bears and mule deer similarly wanes during poor food years or severe winters, respectively, when animals are presumably experiencing additional stress (Johnson et al., 2015; Sawyer et al., 2017). Wildlife often temporally shift their activities to avoid periods of high human activity, for example becoming more diurnal or nocturnal (Gaynor et al., 2018). In our study system, however, insect harassment, which causes caribou to increase their movement rates, is most prevalent during midday when air temperatures peak, overlapping with the same time that traffic levels are also high (Appendix S1: Figure S7). In a post hoc analysis, we used GAMs to estimate variation in caribou step lengths and road-crossing probability as a function of the time of day (instead of traffic, as they are correlated; Appendix S1: Figure S4). As expected, both caribou step lengths and road crossings increased during midday when insect activity was increasing (Appendix S1: Figure S7), suggesting that caribou are unable to temporally separate their movements across roads from the times of day with greater traffic volumes.

Information on the influence of human activity on wildlife can be important for identifying mitigation strategies (Northrup et al., 2012) and is of particular interest in the Alaskan Arctic as global energy needs are spurring new development projects (Fullman, Sullender, et al., 2021; Russell et al., 2021). For example, on federal lands on the North Slope of Alaska, recent environmental planning documents require vehicle use plans for new development projects (BLM, 2019, 2020a, 2020b), which our results can help inform. While response thresholds are often employed to identify tolerable levels of human activity, we found that CAH behavioral responses to traffic were largely continuous, with road crossings declining in response to higher traffic levels without exhibiting clear threshold effects. An obvious solution could be to limit the traffic volume on the road system (Curatolo & Murphy, 1986; Murphy & Lawhead, 2000), and our results suggest that a reduction of any amount could be beneficial. Conversely, instead of stipulating limits on traffic levels, another possible mitigation strategy may be to restrict vehicle traffic during certain times of year (Boulanger et al., 2020; Murphy & Lawhead, 2000) or times of day, when caribou are crossing roads more frequently. For example, CAH caribou primarily interact with roads during the mosquito harassment season between ~10:00 and 18:00, when insect harassment also peaks (Appendix S1: Figure S7). Reducing traffic during this time of year and day could significantly increase caribou movement and enable access to foraging and insect relief habitat. Additionally, in planning future developments, the layout of infrastructure, such as locations of camps, pads, and facilities, could be optimized to minimize required traffic, and operations could be designed to reduce required vehicle visits to remote structures (Holloran et al., 2015; Murphy & Lawhead, 2000; Sawyer et al., 2009).

Our study demonstrates that caribou change their behavior in response both to the road footprint and to traffic, but it is unclear whether these changes manifest in fitness consequences. The CAH migrates to the coastal plain in the summer to take advantage of the productive, albeit short, growing season and abundant protein-rich forage during their calf-rearing and lactation period (Johnson et al., 2021, 2022). Indeed, when they arrive on the coastal plain, their body condition is at its annual minimum (Cook et al., 2021), and they must amass key forage resources while also avoiding insects, infrastructure, and human activity. Murphy and Curatolo (1987) and Nellemann and Cameron (1998) suggested that altered behaviors due to roads and traffic could have nutritional costs and subsequent fitness consequences resulting from the exclusion of caribou from desired habitats. To investigate this issue, Arthur and Del Vecchio (2009) conducted a 6-year study to compare CAH calving parameters between the western portion of the range, where energy development is concentrated, and the eastern portion of the range, where development is minimal. They found that calves in the west were smaller and lighter than those in the east but that there were no significant differences in survival rates. Given that the influence of development on wildlife may depend on variation in environmental conditions or population density

(Sawyer et al., 2017) and can be variable or weak (Kemink et al., 2019), future work on this issue is warranted.

To examine caribou responses to roads, we implemented several novel analytical methods that may be useful in assessing wildlife responses to development in other systems. For example, we did not have traffic data for every road segment in our study area, so we produced fine-temporal-scale traffic volume estimates across the entire road network using boosted regression trees (Friedman, 2001, 2002; Hastie et al., 2009). This approach is known to produce models with high predictive accuracy, and it enabled us to significantly expand the spatial extent of our study. Additionally, we used nonlinear step selection models, which have not been used extensively for SSF analyses. Admittedly, these GAMs are much slower to run than their linear counterparts (e.g., "clogit" in the survival package; Therneau, 2022), but the added flexibility of being able to include nonlinear responses, tensor product interactions, spatial autocorrelation, and regularization (Wood, 2017) may be a worthwhile tradeoff for some studies. The nonlinearity allowed for more flexible responses common in ecological relationships (Austin, 2002; Oksanen & Minchin, 2002; Yee & Mitchell, 1991), while the tensor product interactions allowed for nonlinear interactions, and the spatial autocorrelation term helped account for residual correlation due to the clustering of individuals (e.g., herding) unrelated to our habitat covariates (Bivand et al., 2008; Wood, 2017). Lastly, we also accounted for the spatial layout of the road system in our base models by including road density, which has generally not been done. Because the road system was not random across the landscape and some characteristics were confounded with the road configuration (e.g., traffic is greater near main camps where there is also more roads), this helped isolate the specific effects of road distance and traffic on caribou behavior.

Our study provides a robust analysis of caribou responses to oil field roads and traffic, but there were some key limitations that are important to acknowledge. For example, caribou GPS collars obtained locations every 2 h, and while we assumed animals moved in a straight line between successive locations, the actual movement paths were uncertain. As a result, we expect that more frequent locations would likely strengthen inferences about caribou space use and road-crossing behavior. Additionally, Joly et al. (2021) suggested evaluating the effects of speed restrictions on caribou behavior, and past evidence suggests that may be a useful mitigation measure (Horejsi, 1981). In the Kuparuk and Milne Point oil fields, however, traffic speeds were relatively constant, with a general speed limit of 72 km/h (though slower near pads, facilities, and camps), precluding us from investigating that issue. Also, while visual stimulus of moving vehicles is likely an important factor, noise from traffic and industrial activities can have significant impacts on wildlife (Barber et al., 2010; Blickley, Blackwood, & Patricelli, 2012; Shannon et al., 2016; Ware et al., 2015) and represents an information gap in our system. Additionally, assessing nonroad infrastructure such as pipelines, camps, and pads was beyond the scope of our objectives, but this can certainly influence caribou behavior (Curatolo & Murphy, 1986; Johnson et al., 2020; Prichard et al., 2020) and may warrant further study. Also, group size and maternal status (with or without a newborn calf) was unknown in our study system due to the remote nature of our monitoring, but larger groups and groups with more calves may respond more strongly to anthropogenic disturbance (Curatolo & Murphy, 1986; Murphy & Curatolo, 1987; Smith & Cameron, 1985) and could be investigated. While our results are relevant to caribou behavior during the summer, we expect responses to roads are likely to differ during other times of the year, such as migration periods (Wilson et al., 2016) or winter (Johnson & Russell, 2014). Lastly, we only collected 2 years of traffic data, so we were unable to account for the full range of annual variation in habitat conditions, weather, insect abundance, and CAH abundance on caribou behavioral responses, and we expect more years of data would strengthen our inferences.

As anthropogenic infrastructure and activities become more prominent in landscapes across the globe, it will become increasingly important to mitigate their effects on wildlife (Northrup & Wittemyer, 2013; van der Ree et al., 2011; Vors & Boyce, 2009). While wildlife responses to the footprint of human infrastructure are commonly assessed (Fullman, Wilson, et al., 2021; Johnson et al., 2005; Prokopenko et al., 2017), data on human activity levels are often limited and difficult to collect, resulting in few studies that evaluate their influence, despite their demonstrated importance (Larson et al., 2016; Wisdom et al., 2018). By collecting data on hourly vehicle traffic, we were able to elucidate the individual effects of road infrastructure and road activity on caribou behavior in the Arctic, finding that caribou responded to both aspects of energy development. Although the impacts of infrastructure itself may be difficult to mitigate, there is great potential to alter human activity (e.g., vehicle traffic) to promote caribou movement and road-crossing success within developed landscapes, especially during specific times of year and day. Such information can also be used in future land-use planning and mitigation efforts to minimize the negative behavioral responses of caribou to energy development, which will be critical as industrial activities expand in sensitive Arctic landscapes.

## ACKNOWLEDGMENTS

We thank the Alaska Department of Fish and Game, ConocoPhillips Alaska, Inc., and ExxonMobil for providing caribou location data. We also thank ConocoPhillips and Hilcorp Alaska, LLC, for supplying spatial data on energy development and for enabling us to collect traffic data along the road system. We appreciate M. Arimitsu, L. Parrett, B. Lenart, S. Jones, H. Savage, J. Eisaguirre, P. Cross, and anonymous reviewers for feedback on our analyses and interpretation. This project was part of the USGS Changing Arctic Ecosystems Initiative and was supported by funding from the Land and Species Management Programs of the USGS Ecosystems Mission Area and from the Bureau of Land Management. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. government.


## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Traffic data (Severson et al., 2023) are available from the USGS Alaska Science Center at https://doi.org/10.5066/P9HXW3N5. Caribou location data are managed by Alaska Department of Fish and Game (ADFG) and restricted from public access by Alaska Statute 16.05.815; interested parties can request 2-h caribou GPS collar data from adult females in the Central Arctic Herd between 12 June and 11 August 2019 and 8 June and 19 August 2020 from the ADFG Fairbanks office (https://www.adfg.alaska.gov/index.cfm?adfg=contacts.emailus). Infrastructure data in the Kuparuk oil field supporting this research (i.e., roads, facilities, pads) can be requested from ConocoPhillips Alaska, Inc. (https://www.conocophillips.com/contact-us/). Infrastructure data in the Milne Point oil field supporting this research (i.e., roads, facilities, pads) can be requested from Hilcorp Alaska, LLC (https://www.hilcorp.com/contact-us/). All other data sets used in the analyses are available through sources cited in the text, including: landcover from the Alaska Center for Conservation Science (https://accs.uaa.alaska.edu/files/data/AlaskaVegetationWetlandComposite.zip); elevation from the USGS National Map (https://www.usgs.gov/the-national-map-data-delivery; 3DEP, 1 arc second); streams from the USGS National Hydrography Dataset (https://prd-tnm.s3.amazonaws.com/StagedProducts/Hydrography/NHD/State/Shape/NHD_H_Alaska_State_Shape.zip); and weather data (10 m wind: u-component and v-component; 2 m temperature) from Muñoz Sabater (2019) available in the Copernicus Climate Change Service (C3S) Climate Data Store (CDS) at https://doi.org/10.24381/cds.e2161bac. Our code was not novel, and the functions and packages we used are available from the sources cited in the text.


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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Severson, John P., Timothy C. Vosburgh, and Heather E. Johnson. 2023. "Effects of Vehicle Traffic on Space Use and Road Crossings of Caribou in the Arctic." *Ecological Applications* 33(8): e2923. https://doi.org/10.1002/eap.2923